

# Causes of large-scale eucalyptus tree dieback and mortality: research priorities

A report for the NSW Natural Resources Commission

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# TERG

TERRESTRIAL ECOLOGY  
RESEARCH GROUP



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## Executive Summary

Canopy dieback in eucalypts across southern Australia, including all of New South Wales (NSW), has been widely recorded and generated substantial debate regarding appropriate management responses. Canopy dieback in eucalypts was first reported in the 19<sup>th</sup> century with substantial episodes in NSW in the 1950s and 1970s with continued episodes across a range of settings. Canopy dieback has been reported from most forest types and land uses, though with particular ferocity in landscapes experiencing some form of anthropogenic change (fragmentation, fire regime, weed invasion, waterlogging, nutrient inputs, etc). As a phenomenon, canopy dieback in eucalypts has always occurred as a stress response to changing growing conditions. Eucalypts, and many broad-leaved trees, are able to re-adjust their growth and form as their conditions change, which is in contrast to the well-studied conifers of the northern hemisphere which tend to experience total tree mortality when stressed. Over the past 100+ years, and particularly in the last ~50 years, scientists have studied eucalypt dieback events from a variety of disciplines and perspectives. Investigations have taken a variety of approaches and experimental designs spanning observational approaches, correlative associations, and confirmatory experiments among others. In this review, we were tasked with:

- 1) Synthesising the existing literature of eucalypt dieback
- 2) Weighing the relative strength of evidence
- 3) Identifying key knowledge gaps
- 4) Prioritising future scientific research likely to yield *relevant on-ground management* insights within NSW

In this document, we first examine history of eucalypt dieback in southern Australia and the ecosystem services threatened by canopy dieback in forests and individual trees in rural landscapes (urban/suburban settings were excluded). We then examine the importance of experimental design and inference relative to the complexity of eucalypt dieback. This is a crucial issue because of the potential to misdiagnose causative factors and the precious limited resources available to support informed land management. The key topics we examine are: bushfire, drought, leaf-feeding insects, nutrient disorders, land use and management (including planned fire), and other stressors less important in NSW. In all sections we identify the relevant literature and proposed mechanisms followed by the primary and currently active researchers, areas of contention and agreement, whether the mechanism is a proximate or ultimate driver of canopy dieback, and key knowledge gaps for future research activities.

### Research Priorities:

Across all research priorities, key principles to be embraced are interdisciplinary approaches and strong experimental design able to draw strong inference. Further, in light of the 2019-2020 bushfire season, we encourage scientists to consider opportunities to draw on existing data where re-measurement of impacted plots (particularly those having experienced past canopy dieback) offers opportunities for strengthened insight, particularly for land managers. Following our review of the literature, we identified the following research themes most likely to yield relevant on-ground management actions within NSW:

- Retrospective research that explores the relationship between dieback events and past climatic events in recent history (i.e. fusing of field and remote sensing data types)
- Retrospective research offering novel insights into past disturbance regimes (heat waves, drought, fire) to contextualize the future. In particular, efforts to document Aboriginal knowledge and histories regarding past climate and fire as well as modern dendrochronological efforts to reveal patterns of past climates and fire frequencies
- Research into the effectiveness of interventions to suppress undesirable feedback loops and re-establish positive feedbacks and trophic coherence
- Research that investigates the functional attributes of eucalypts that make them both more vulnerable or less susceptible to dieback (for example: waterlogging susceptibility)
- Research that investigates the biogeochemical relationship between low intensity fire and eucalyptus vulnerability to dieback and how it may be moderated by soil biota
- Quantification of ecosystem services losses due to eucalypt dieback, including cultural loss for Indigenous people
- Investigation of dieback events that occur at large spatial scales, and with severity where it may pose the highest risk to species, native communities, and ecosystems services (Figure 1)
- Research located in rural regions where native eucalypt communities are severely fragmented, and their value is outsized (for example: accelerating loss of scattered mature trees in paddocks) and likely offer substantial value for money
- Research engaged with complex diebacks where understanding may take substantially more research effort than either simple or two-factor diebacks (Figure 2)

# Introduction

## Overview

Dieback events in eucalypts<sup>1</sup>, where the tree crown variously retracts, yellows, wilts, or otherwise is reduced, have been documented in Australia since the 19<sup>th</sup> century and subsequently across all regions of Australia, especially in the southern temperate zone (White 1966). The Society of American Foresters (1950) defined the term ‘dieback’ as “progressive dying back from the tips of twigs, branches or tops” and we adopt this further including loss of stems and roots (Podger 1981). Repeated dieback events, in the absence of full recovery, lead to progressive eucalypt decline and tree mortality.

## History of eucalypt dieback

Eucalypt dieback, as defined here (i.e. a tree symptom), is not a new phenomenon, and has very likely always occurred. One of the earlier documentations of widespread and severe dieback was recorded by Norton (1886) in the New England Tablelands of New South Wales (NSW) in the 1850s. Between 1852 and 1857, Norton (1886) observed thousands of acres affected by multiple dieback events, associating them with frost (*Corymbia gummifera*, in the headwaters of Burnett River), soil changes from intensive sheep grazing, drought, waterlogging, woodborer infestation, and seasonal defoliation of *E. viminalis* by “thousands of small beetles”. White (1966) describes insect outbreaks and dieback events affecting *Eucalyptus fasciculosa* in South Australia from 1914-1920. By the 1920s in Western Australia, widespread dieback was prevalent throughout large portions of *E. marginata* forest following a period of rampant timber exploitation (Davison 2015). Clark (1962) provides one of the first documented cases of insect-driven dieback; a widespread and sustained psyllid (*Cardiaspina* spp.) outbreak in the Southern Tablelands and Slopes region, lasting over 10 years through the 1950s. Such psyllid outbreaks have continued off-and-on throughout large portions of southeastern Australia to present times (White 1966, Stone 2005, Hall et al. 2015). Widespread and severe eucalypt dieback events from a variety of drivers were reported throughout Australia in the 1960s and 1970s (Ellis 1964, Cremer 1966, Pook et al. 1966, Marks et al. 1972, Bird et al. 1974), leading to public concern (Sinden et al. 1982). A working group was assembled to investigate dieback in the New England Tablelands in 1976, and results from subsequent surveys were reported to the Minister (Mackay et al. 1984). A conference focused on eucalypt dieback events was convened in 1980 in Canberra to discuss the phenomena, and many of the most pressing dieback events were outlined from each state (Old et al. 1981), including a variety of studies concerning events in NSW (Carter et al. 1981, Ford 1981, Roberts and Sawtell 1981, Williams and Nadolny 1981). Since that

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<sup>1</sup> Eucalypts which are almost entirely restricted to Australia, broadly include seven genera (*Eucalyptus*, *Corymbia*, *Angophora*, *Stockwellia*, *Allosayncarpia*, *Eucalyptopsis*, *Arillastrum*), but in practice refer to *Eucalyptus* and *Corymbia*, the two largest and most widespread genera.

time, dieback events appear to have continued and intensified in certain regions (Evans et al. 2013, Brouwers and Coops 2016), expanding to more species and contexts (Ross and Brack 2017). Forest surveillance systems and research studies on dieback have shifted since the 1980s from those that observe and describe phenomena to a combination of focused intra- and interdisciplinary investigation of individual associated factors or interactions between factors. For this, and other reasons (e.g. changes to forest department staff), individual events are not being observed and described in a systematic fashion (Robinson 1998), as they had previously, making it difficult to assess whether incidence of dieback events are increasing over-time.

### *Characteristics of tree dieback*

While dieback can occur as part of the normal aging process and senescence (Franklin (Franklin et al. 1987, Mueller-Dombois 1987), most dieback events are triggered by changes in the growing environment prior to full maturity (Das et al. 2016). Tree dieback may be complete dieback, causing the death of the tree, or incomplete, resulting in partial tree dieback (Jump et al. 2017). Tree dieback, including crown and canopy dieback are amongst the most well-documented tree conditions in the world (Ciesla and Donaubaauer 1994). Eucalypts commonly exhibit signs of partial tree dieback in response to external stress, stopping short of tree mortality (Burrows 2013). In contrast, most conifer and many broadleaved species of other genera lack the ability to partially dieback and resprout (Vesk and Westoby 2004) with tree mortality in these genera common following stress events (Allen et al. 2010). Eucalypts, however, are among the most resilient trees in the world, and are exceptionally well adapted to resist and recover from significant partial tree dieback (Burrows 2002). For this reason, mature eucalypts in the absence of severe disturbance (wildfire, flood) have historically low tree mortality rates in their native ecosystems ( $< 1\% \text{ yr}^{-1}$ ) (Wellington and Noble 1985, Abbott and Loneragan 1986, Taylor et al. 2014). Partial tree dieback can represent an opportunity for trees to re-equilibrate and adapt to their external environment (Schwilk et al. 2016). Indeed, in healthy stands of eucalypts, in dynamic equilibrium with their fluctuating environments, some degree of branch dieback and epicormic recovery is always present as an adaptive response to the vagaries of weather and the activities of pests and parasites (Podger 1981). The ability to partially retract enables trees to survive stressors that would otherwise lead to death in conifers and many non-eucalypt broad-leaved trees. Water stress can be reduced or eliminated if trees rapidly reduce their leaf area through the shedding of leaves, shoots, and branches (Rood et al. 2000, Wolfe et al. 2016), though species vary in their capacity to do so. Worldwide, the ability to undergo partial dieback and then recover is generally related to the dynamism of the growing environment, which includes climate, herbivore or pathogen cycles, and disturbance regimes (Del Tredici 2001). The historically variable growing environment in southern Australia, for example, including multi-decadal droughts (Barr et al. 2014), favours plant traits that enable partial dieback and recovery from stressors in eucalypts and other species. Therefore, eucalypt dieback is not inherently a problem *per*

se, and under some circumstances may represent an indicator of a healthy tree and stand response to stress (Bird et al. 1974). That is, low levels of crown dieback can simply represent a structural adjustment to recent environmental change (Magnani et al. 2002, Lapenis et al. 2005). Additionally, trees can alternate between periods of dieback and regrowth when stress is relieved. Commonly, however, repeated dieback events can lead to progressive tree decline and death (Ciesla and Donaubauer 1994) when recovery is incomplete or absent. Progressive eucalypt decline may be non-linear, and can alternate between periods of dieback and regrowth when stress is relieved (Jones et al. 1990); however, crown recovery is incomplete and trees degrade from repeated dieback events. Eucalypt dieback becomes a problem for society, the economy, environment, and culture when the scale, severity, and frequency of dieback significantly impacts ecosystem condition and the ability of ecosystems to provide critical services and resources.

#### *Importance of scale, severity and complexity of eucalypt dieback*

The spatial scale and severity of eucalypt dieback interact to define the risk to societal and environmental services and values (Figure 1). As eucalypt dieback expands across the landscape, and severity increases (Allen et al. 2015), both the number of services and the risk to each service increases. For example, partial crown dieback of individual trees poses a low level of risk to human and wildlife health from falling debris (i.e. hazard trees), with the greatest risk in parks and gardens but little impact on services at coarser community, ecosystem, or landscape scales. In contrast, widespread complete dieback and mortality of a forest may pose a risk to water resources (Brouillard et al. 2016), biodiversity protection (Ford and Bell 1981), tourism (Walters and Clulow 2010), cultural identity (Sinden and Jones 1985), and carbon sequestration (Walden et al. 2019). Understanding that while dieback is a common condition in eucalypts, it is critical to define the scale and severity of eucalypt dieback events in order to better understand potential impacts on services and values. Thus, not all dieback events pose equivalent risks to the society, environment, and culture. In this report, we have focused primarily on those events that are pertinent to southeastern Australia, (particularly NSW), and are widespread and severe, leading to tree mortality across large spatial scales.

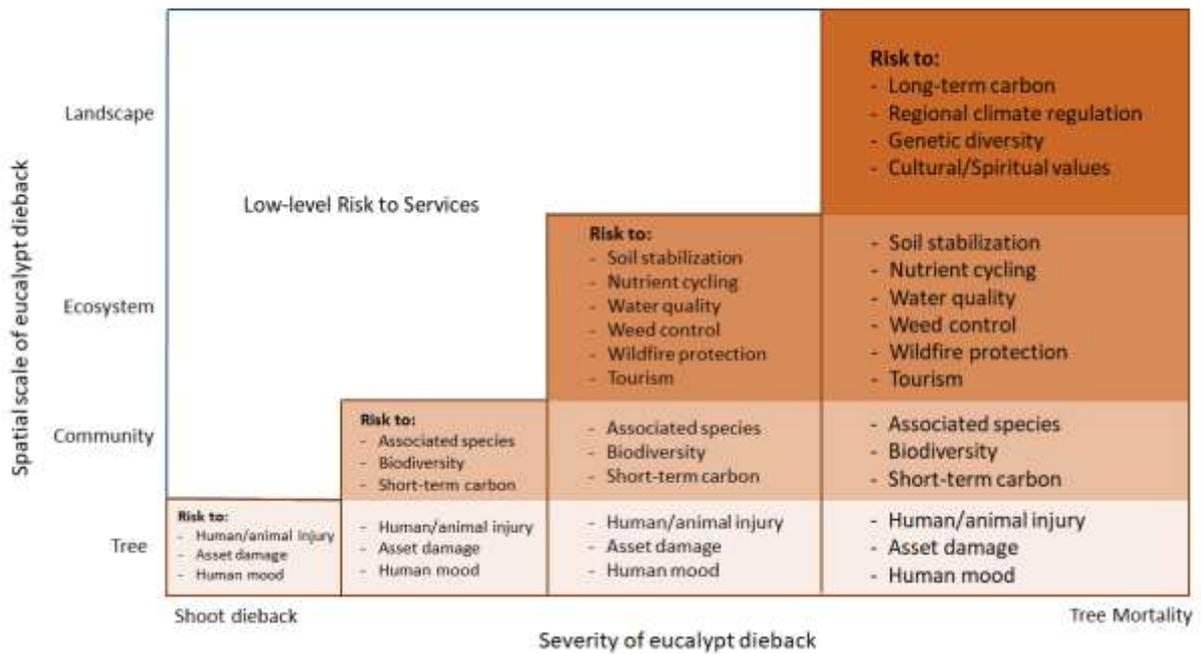


Figure 1: The spatial scale and severity of eucalypt dieback can interact to define the risk to societal, environmental, and cultural services and values.

Eucalypt dieback events can vary considerably in their complexity, and we have categorized them coarsely into three groups, simple, two-factor, and complex (Figure 2). In many scenarios, eucalypts die-back in response to a single stressor, and represent a relatively simple interaction between stress and tree response. Some examples of simple dieback events include those that involve, for example, direct interactions with fire or frost where tissues succumb to extreme high (Matusick et al. 2013, Aspinwall et al. 2019) and low (Paton 1988) temperatures, respectively. A number of other eucalypt dieback events can be explained by the interaction between two stressors, acting synergistically, additively, or one factor facilitating another to cause eucalypt physiology to reach critical thresholds. Examples of two-factor dieback events include those that are caused by the combination of drought and fungal shoot pathogens (Burgess and Wingfield 2002, Carnegie 2007), drought and heat (Matusick et al. 2013), drought and fire (Prior et al. 2016) and waterlogging and *Phytophthora cinnamomi* root disease (Davison 2018), among others. The final category of eucalypt dieback events is more cryptic, and either involve more than two factors, involve a unique sequence of stressors that vary temporally, or involve a positive feedback cycle that amplifies dieback severity. These complex dieback scenarios also predominately occur in degraded or fragmented eucalypt communities, where multiple ecosystem processes are dysfunctional. In the case of this report, we will focus on the latter two dieback categories as most scientific uncertainty and debate pertains to the two-factor and complex dieback situations. Unpacking and determining the underlying cause or complex of causes of these dieback scenarios will be critical in moving towards modelling impacts, planning for increasingly complex environmental conditions, and ensuring adaptation occurs.

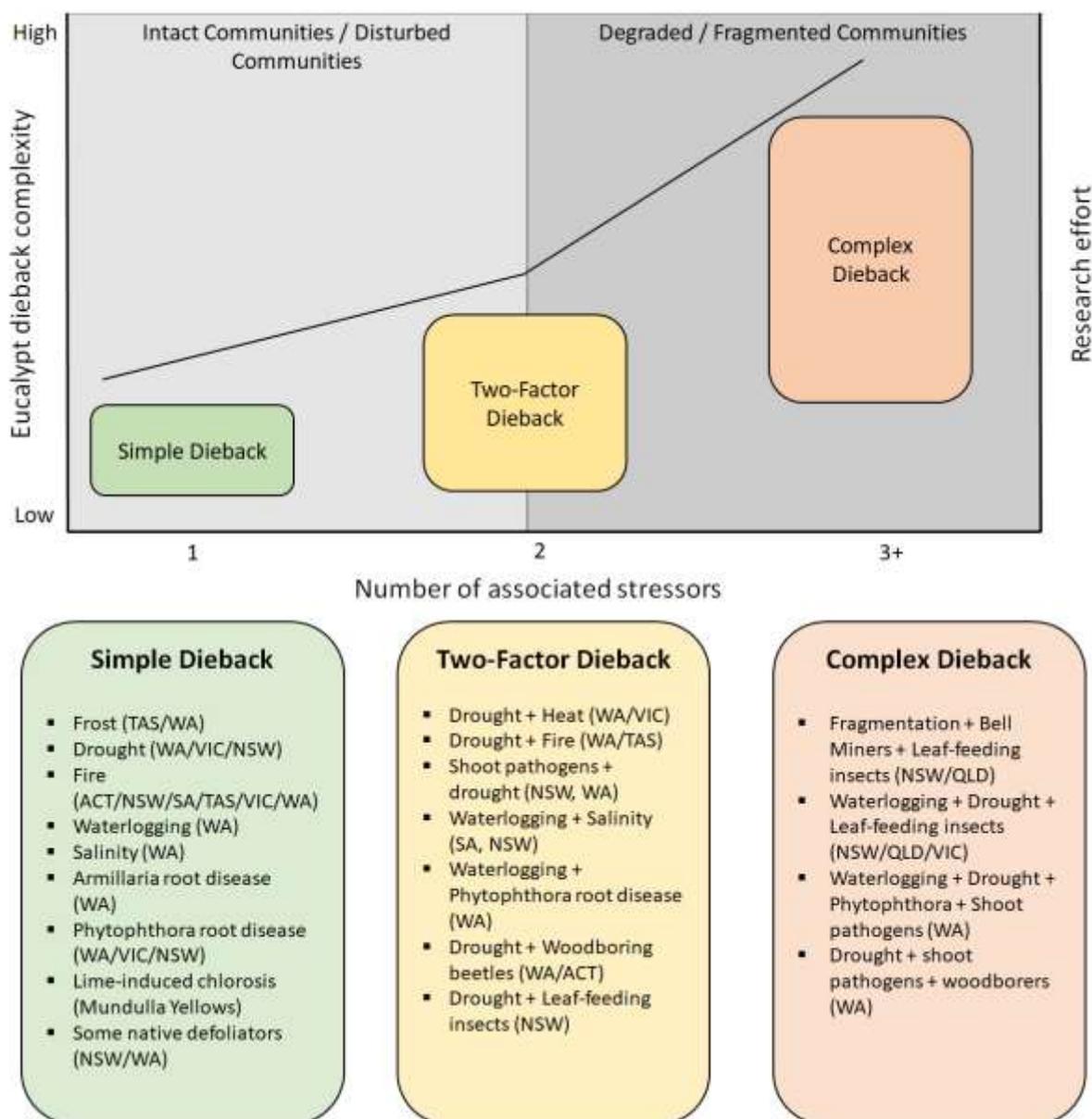


Figure 2. Complexity of eucalypt dieback and associated number of stressors. Lists of examples of each category of dieback are not intended to be comprehensive. Rather, we intended to highlight examples of well-published stressors (or combination of stressors) implicated in dieback, and the Australian states in which they commonly occur.

## Risk of eucalypt dieback to ecosystem services

In NSW and across southern Australia, eucalypt dieback poses a significant threat to a variety of important ecosystem services depending on the scale and severity of the dieback event. The impacts of eucalypt dieback on ecosystem services and resources in rural, mixed land use regions of Australia have been addressed by Reid and Landsberg (2000), while the impacts on services provided by intact ecosystems are less well understood. Considering the historically important ecosystem

services and projecting from analyses elsewhere, we have identified the services likely to be most impacted by eucalypt dieback in southern Australia. Impacts to ecosystem services can interact with one another, with the potential for cascading effects. A variety of ecosystem services and resources are threatened by eucalypt dieback in southern Australia and include provisioning services (e.g. energy, water), regulating services (e.g. climate regulation, flood prevention, erosion control), cultural services (e.g. educational, recreational, tourism, heritage, spiritual) and supporting services (e.g. biological diversity maintenance, nutrient recycling, primary productivity) (IOPT 2010). For example, the loss of foundation tree species from eucalypt dieback can threaten iconic flora and fauna species (Paap et al. 2017b) that are critical to cultural heritage and traditions, which are then eroded (von Brandenstein 1977). *Future work should explore the direct and indirect links between the scale and severity of eucalypt dieback events, and ecosystem services and resources critical to southern Australia.*

### *Provisioning Services*

#### Carbon sequestration

Globally, forests store the vast majority of terrestrial carbon and represent the largest source of climate change mitigation potential (Jackson et al. 2008). Some eucalypt forests in southern Australia are the most carbon-rich forests in the world, making them among the most valuable ecosystems for future climate mitigation (Keith et al. 2009, Volkova et al. 2018). While land clearing for development, tree harvesting for forest management, and wildfire represent the greatest threats to carbon sequestration in southern Australia's forests (Dean et al. 2012, Bowman et al. 2013, Prior et al. 2013), widespread and severe eucalypt dieback can cause significant carbon emissions (Walden et al. 2019). For example, in a eucalypt forest in southwestern Australia, over 49 t ha<sup>-1</sup> of live standing carbon was lost from a single, severe eucalypt dieback event (Walden et al. 2019). Repeated dieback events have the ability to cause tree decline and mortality, additional carbon emissions, and are expected to transform some tall, carbon-rich forests into short, multi-stemmed forests with lower carbon sequestration potential (McDowell and Allen 2015, Matusick et al. 2016a). Furthermore, a positive feedback loop may ensue, with climate change leading to more severe and extensive dieback events, which can alter potential fire behaviour, including increasing the potential rate of spread (Ruthrof et al. 2016), which then generates high carbon emissions (Volkova et al. 2019). For these reasons, eucalypt dieback represents a significant threat to the future carbon sequestration potential of carbon-rich forests of southern Australia.

#### Water resources

All major metropolitan areas in southern Australia have historically relied on forested catchments to provide their water. While recent decentralization of water supply networks has diversified water sources (Coombes and Barry 2008), forested catchments remain an important source

of water for most people in southern Australia (Elmahdi and Hardy 2015). Changes in forest condition (i.e. structure, composition, function, health) have been shown to significantly impact drinking water supply and quality in many areas of Australia (Grigg 2017, Yu et al. 2019). For example, in the Victorian Central Highlands, old-growth mountain ash (*Eucalyptus regnans*) forests yield nearly twice as much annual water as young regrowth forest (Vertessy et al. 2001). The relationship between forest condition and water runoff has driven research into forest management for desired water objectives (Ruprecht and Stoneman 1993, Hawthorne et al. 2013). Additionally, a variety of studies have illustrated the impacts of wildfire on water quality in Australia's catchments (Prosser and Williams 1998, Smith et al. 2011). The direct impacts of eucalypt dieback on water quantity is not well understood. However, a review investigating the ecohydrological consequences of tree die-off worldwide suggests a variety of hydrologic processes are likely to be affected, including infiltration, runoff, groundwater recharge, and streamflow, among others (Adams et al. 2012). The relationship between streamflow and tree mortality is unclear. Under most circumstances, dieback is expected to increase water yields (Adams et al. 2012). However, some observations from dry regions found a reduction in runoff in response to tree die-off (Guardiola-Claramonte et al. 2011). The relationship between tree dieback and water quality has been illustrated elsewhere (Mikkelsen et al. 2013), including in the Rocky Mountains of North America where tree mortality increased organic carbon (Brouillard et al. 2016) and damaging disinfection by-products (Mikkelsen et al. 2013) in stormwater runoff. Depending on the soil chemistry, tree dieback leads to leaching of important ions, surface soil organics (Kopacek et al. 2017), and other potentially damaging elements that alter surface water chemistry (Fayram et al. 2019). These findings suggest that where forest and woodland condition are strongly linked to water resources, widespread and severe eucalypt dieback would have effects on a variety of water characteristics, including the supply and chemistry.

#### Timber wood fibre resources

Timber resources are directly affected by dieback events through the reduction in increment growth (Bird et al. 1974). In 1959-1960, for example, in Southeastern Tasmania, *Eucalyptus obliqua* and *E. regnans*, experienced widespread dieback associated with drought and attack by secondary pathogens. The estimated loss in volume was between 0 (in unaffected plots) to a maximum of 142 m<sup>3</sup>/ha (in affected plots), and it was concluded that the total loss in value during the 1960-70 period in that 16,000 ha of production forest was < \$2 million (West and Podger 1980). In central Victoria, in the mid-1970s, dieback affected approximately 1400ha of high-quality production forest of *E. obliqua*, *E. viminalis* and *E. globulus* subsp. *bicostata*. Losses per unit area were estimated to be in the range from 0.3 to 2.0 m<sup>3</sup> ha<sup>-1</sup> yr<sup>-1</sup>, depending on site and severity of dieback. Stands with severe and moderate dieback are estimated to have respective sawlog volume increments of about one half and two thirds that of an average healthy stand. Losses of this order are cause for concern since both dieback severity and extent are increasing (Edgar et al. 1976). Mazanec (1966, 1967) described

phasmid attacks (*Didymuria violescens*) on *E. delegatensis* and *E. regnans* in southeast Australia that reduced growth; in 1962-1963, about 3000 acres of immature *E. regnans* was defoliated, and by 1964 about 100 acres appeared to be dead. Eighty percent of the trees died, and diameter increment in survivors was negative for two years (Felton 1972). However, the overall cost of this insect attack was not quantified. Impacts on timber yields have implications for regional communities as timber and forest projects are key to supporting economic and social viability of regional economies. The Forestry Corporation of NSW (Forestry Corporation) manages a timber business and underpins the operations of processors, mills, contractors, suppliers and related business in regional communities (FCNSW 2019).

### *Cultural Services*

#### Tourism

Tourism is among the biggest industries in Australia, generating \$131.4 billion in 2017-2018 (TRA 2019). New South Wales and Victoria dominate the tourism industry in Australia, representing a combined 58% of the total money spent (TRA 2019). Since nature-based tourism represents a major driver of visitors to regional Australia, maintaining healthy ecosystem condition is an important factor in the sustainability and growth of the industry. There are no studies examining the direct effects of eucalypt dieback on tourism. However, studies of other natural disasters in Australia illustrate that the tourism industry suffers from failing ecosystem health, amplifying economic strain on regional Australia (Walters and Clulow 2010, Richardson et al. 2012). For example, the loss of revenue for the tourism industry in Queensland following the floods and Cyclone Yasi of 2010-11 was estimated to be \$590 million (Richardson et al. 2012). Results from both the Queensland floods and 2009 Black Saturday Fires in Victoria show that dramatization and mischaracterization of the disaster by the media significantly influences tourist perceptions and visitation behaviour (Walters and Clulow 2010, Walters et al. 2015). For example, despite the fact that the Black Saturday fires only affected 2.5% of the Gippsland region, the tourism industry throughout the region suffered due to tourist perceptions of the disaster, with an estimated income loss of \$44 million; early media reports following the historic 2019-2020 bushfire season suggest even larger losses. This underscores the importance of understanding and accurately characterizing the scale and severity of natural disasters. Despite the dearth of directly-applicable research on the topic, it is not difficult to project a significant loss of tourism to regions affected by widespread and severe eucalypt dieback events.

#### Cultural identity

Australian Indigenous culture is the oldest living culture on the planet, and has a long, deep and continued connectedness to, use, and occupation of forests. Cultural and spiritual heritage includes not only the physical and spiritual sites, but places, objects, stories, oral histories, flora, fauna and documents relating to Aboriginal occupation before and after European contact (ForestsNSW

2010, Pascoe 2018). Forests contain plants used as food, medicine and properties such as sap and fibre for the creation of tools such as shields, canoes and carriers. or animals that are totems or sought for food. The habitats that support this flora and fauna are important to Aboriginal people (ForestsNSW 2010). Aboriginal communities place spiritual and cultural value on locations because they feature in dreaming stories or because of historic events or traditions linked to the land, such as initiation or birthing sites (ForestsNSW 2010). Access to forests and the ability to visit special places is critical for cultural survival(NRC 2019). Furthermore, there exists an extensive knowledge system regarding forest management, including about ecological processes and cycles, and interactions with fire. Indeed, almost all researchers now accept that Australia’s Aborigines were managing their country with the broad-scale use of fire when Europeans arrived (Gammage 2008)

In modern times, images of thin-crowned eucalypts lining paddocks or in open woodlands, some with dead empty branches, are among the most recognizably Australian images for many people around the world. These scenes illustrating eucalypt dieback simultaneously portray the harshness of the environment and the resilience of the species living in it. This combination of suffering and resilience is emblematic of the Australian people, both Indigenous and colonial (Bragg and Reser 2012). In a sense, the presence of low levels of partial dieback in eucalypts may provide more to define Australian cultural identity than threaten it. While formal analyses of the impact of eucalypt dieback on critical societal attributes have been lacking, they have been part of the debate (Sinden and Jones 1985). Eucalypt dieback is likely to pose a threat to the cultural identity, aesthetic, and heritage when the scale and severity increases and resilience falters. When eucalypt dieback escalates to the point of widespread tree mortality, once familiar, comforting landscapes can be transformed into alien environments and degrade cultural identity, community psyche, and “sense of place” (Rogers and Bragg 2012).

### *Supporting Services*

#### Biodiversity protection

Southern Australia contains some of the most biodiverse ecosystems on the planet (Hopper and Gioia 2004), contributing to Australia’s status as a megadiverse country and continent. Given the role of eucalypts as keystone species in many areas (Manning et al. 2006, Stagoll et al. 2012), a significant share of the worlds’ biodiversity (including the maintenance of genetic resources) is reliant on well-functioning eucalypt trees, forests, and woodlands for survival. Most studies relating eucalypt dieback with changes in associated flora involve invasion by *Phytophthora* root pathogens or drought (Kirkpatrick and Marks 1985, McDougall et al. 2005), which directly affects susceptible understory species (Shearer et al. 2004), and can cause dramatic changes to vegetation communities (Pook et al. 1966, Shearer and Dillon 1996, Weste 2003). The indirect effects of eucalypt dieback on flora, however, are more subtle and much less well understood. For example, severe eucalypt dieback causes higher near-ground solar radiation, surface wind, and temperature (Ruthrof et al. 2016), which

may disrupt the competitive dynamics of the forest understory (Volkova et al. 2009). Furthermore, if dieback is severe enough, and substantial changes in plant-available resources occur, areas may become more vulnerable to invasive species, further reducing suitable habitat.

A variety of studies have observed changes in fauna abundance and behaviour in association with eucalypt dieback in southern Australia (Montague-Drake et al. 2009, Moore et al. 2014b, Anderson et al. 2020). Suites of faunal species can have very different responses to changes in eucalypt condition (Moore et al. 2014a). For example, cockatoos can benefit from dieback in the short-term by feeding on woodboring beetles invading affected trees (Robinson 1965), while honeyeaters and other foliage feeders are likely negatively impacted by eucalypt dieback, since they prefer to forage in tall trees with adequate leaf area (Moore et al. 2013). In the forest and woodland environment, many faunal species can adapt to changing conditions resulting from eucalypt dieback, particularly when dieback is incomplete (less severe). Areas where species of conservation concern are reliant on a limited supply of existing habitat may be particularly susceptible to biodiversity loss when eucalypt dieback events occur (Manning et al. 2006, Montague-Drake et al. 2009).

## Challenges and disciplinary approaches to the study of eucalypt dieback

### *Major challenges in studying eucalypt dieback*

Determining the causal factors of eucalypt dieback events is challenging due to the complexity of ecological systems. Tree age and growth history have increasingly been recognized as important factors in tree diebacks and declines in North America and Europe (Cailleret et al. 2014, Ireland et al. 2014). The combination of dynamic growing environment in southern Australia and opportunistic growth habits of eucalypts (Schweingruber 1992, Argent et al. 2004) undermines most traditional dendrochronological (tree ring analysis) techniques (Heinrich and Allen 2013). Therefore, understanding the role of age-related stress in eucalypt diebacks is out of reach for most settings and researchers. Additionally, symptoms are not always recognized quickly, research funding and resources are allocated slowly, and external stress agents are temporally and spatially dynamic. The combination of these factors means that some studies are undertaken after the causal stress has been relieved and evidence of the causal stress agent is gone, further challenging successful attribution of eucalypt dieback drivers (Landsberg and Wylie 1983, Scott et al. 2012). Additionally, stress factors can interact with one another in space and time to amplify tree stress (Kasson and Livingston 2012, Sangüesa-Barreda et al. 2015, Dashiell et al. 2017, De Grandpré et al. 2019). In these instances, understanding a single stressor is not adequate to explain the source of dieback, and can result in misleading or incorrect diagnoses (De Grandpré et al. 2019). For example, historically weak stress agents may interact to amplify stress and mortality (Wood et al. 2018). Finally, tree dieback events

can result from a process or cascade of events (Kasson and Livingston 2012), including multiple interactions between predisposing, contributing, and causal factors (Kolb and McCormick 1993). In some cases, the start of these processes occurred weeks, months, or years prior to any visual signs of dieback (Sangüesa-Barreda et al. 2015). Therefore, understanding the history of disturbance and site changes can be crucial (Pook 1985, Ashton and Spalding 2001), which is difficult in eucalypt ecosystems where dendrochronologies (tree ring records) are unavailable and site records are sparse.

### *Disciplinary approaches*

Given the range of challenges in diagnosing eucalypt dieback, traditional intradisciplinary research approaches may not be adequate for understanding many dieback events. The long research history regarding eucalypt dieback illustrates these limits of the intradisciplinary perspective, including competing research narratives into the causes of certain eucalypt diebacks (Podger 1972, Davison 2015, Ross and Brack 2015, Jurskis 2016, Ross and Brack 2017). By recognizing that eucalypt trees may be coping with a range of stressors at any time, it is not difficult to imagine that single-stressor examinations will fail to produce plausible explanations for and solutions to many dieback events (Niinemets 2010). These types of phenomena, including a range of disparate factors interacting in space and time, may be most successfully treated using interdisciplinary and transdisciplinary research approaches (Albrecht et al. 1998, Buizer et al. 2015). With complex phenomena, a complete dissolution of disciplinary research boundaries and perspectives can result in a completely new paradigm, which would not have been possible evolving from a single discipline (i. e. transdisciplinarity) (Max-Neef 2005). Interdisciplinary and transdisciplinary research strategies have demonstrated the capacity to comprehensively examine and provide practical solutions to complex phenomena, including groundwater (Scholz et al. 2000), fire (Carmen et al. 2011) and grazing management (Sherren et al. 2010). While achieving transdisciplinarity may be difficult, time-consuming, risky, or not always possible or necessary to achieve proximal research aims (Ramadier 2004, Christie 2006, Zscheischler and Rogga 2015), striving for the total integration of multiple interacting component disciplines may be a worthy goal when intradisciplinary approaches have failed to produce useful outcomes. In summary, the history of the mainly intradisciplinary approach to certain eucalypt dieback events have produced conflicting narratives in certain cases, and combined with the clear complexity of these phenomena, makes them good candidate systems for inter- and trans-disciplinary science. For complex dieback events, the degree of disciplinary integration may relate directly to the likelihood of success in diagnosis, and development of lasting management outcomes.

## Research methods for eucalypt dieback and our approach

### *Overview of research methods*

A wide range of research methods and approaches are represented in the extensive literature base concerning eucalypt dieback. As in any field of research, the research methods and approaches used to study eucalypt dieback determines the scope of inference and strength of findings. For example, a paper that describes a eucalypt dieback event occurring in one specific place and at one specific time provides valuable information on eucalypt condition, helps narrow down the possible primary causes of the dieback, and potentially provides enough information to develop hypotheses. In contrast, a paper that undertakes a well-replicated and controlled experiment in a glasshouse, aimed at testing specific hypotheses regarding the eucalypt dieback, can determine whether the tested factors can cause dieback. While both example studies are important to understanding eucalypt dieback, they differ dramatically with respect to their scope of inference and strength of findings. In this review, our approach is to not exclude any research on the topic of eucalypt dieback; each paper has a role to play in explaining the phenomena. Furthermore, there are naturally a range of barriers that exist when it comes to research methods and approaches; scope of inference and strength of findings can be limited by the design which are often limited by feasibility and expense. However, we aim to focus most attention on the findings from those studies that have the greatest scope of inference and strength of findings, which are primarily defined by their research methods, sampling design, and approaches. In the following section we review the range of research methods that have been used to study eucalypt dieback, and outline their relative scopes of inference, strengths of findings, and roles in future research.

### *Observational studies*

Most studies on eucalypt dieback are observational, examining a dieback event in a specific place or region, and at a specific time (Carnegie 2007, Davidson et al. 2007, Close et al. 2008, Nageli et al. 2016). In some cases, studies have been purely descriptive with no attempt to identify multiple conditions, locations, or isolate any variability necessary for systematic evaluation (Semple et al. 2010, White 2014). In these instances, the scope of inference is quite limited and the ability to determine associations between stressors and dieback is weak. The remainder, and majority, of the observational studies have used a systematic design, including observing multiple dieback conditions (e.g. severe dieback, mild dieback, no dieback) (Nageli et al. 2016). Systematic observational studies have been focused on developing associations between stressors and dieback symptoms (Stone 2006, Stone et al. 2008). While these studies are generally very effective at identifying potential causal factors, they are unable to conclusively identify the cause(s). Generally, one or more plausible hypotheses for the cause(s) of eucalypt dieback are developed from systematic observational studies (Landsberg and Wylie 1983, White 1986, Davidson et al. 2007, Close et al. 2009). Depending on the situation, including size of the region studied, level of replication, number of dieback conditions, and sampling approach, hypotheses developed from systematic observational studies can have different

strengths. Systematic observational studies commonly represent a critical first step in understanding novel eucalypt diebacks, and are likely to continue to play an important role in future research landscape.

#### *Longitudinal observational studies*

Some observational studies have utilized the strength of longitudinal study designs, observing changes in tree and forest condition over time, to answer questions regarding the eucalypt dieback and recovery processes (Mackay et al. 1984, Jones et al. 1990, Ashton and Spalding 2001, Hanold et al. 2006, Souter et al. 2014). Most commonly, these studies are established after symptoms have developed, tracking continued tree dieback and canopy decline or recovery (Pook and Forrester 1984, Hanold et al. 2006, Souter et al. 2014). Studies have generally not observed the entire dieback process, by repeatedly measuring from preceding the dieback event through to recovery or mortality (Saunders et al. 2003). Some studies have been able to infer the pre-dieback forest condition by arriving shortly after the onset of symptoms (Matusick et al. 2013, Li et al. 2018a). By repeatedly measuring sampling units, rates of change can be determined (Mackay et al. 1984, Mogoutnov and Venning 2014), which is required for developing modelling tools or assessing model predictions (Medlyn et al. 2016) and understanding of disturbance effects. Longitudinal observational studies can have a wide scope of inference and high research strength. Similar to other observational studies, causal factors cannot be conclusively determined. However, by making repeated observations on the same sampling unit, there is greater statistical strength than observations made at a single point-in-time.

#### *Experimental studies*

Specific hypotheses are tested using experimental approaches. Commonly, experiments occur in simplified systems and controlled environments, including glasshouses or plantations, in an attempt to isolate specific factors (Landsberg 1990c, Creek et al. 2018, Ahrens et al. 2019, Hossain et al. 2019). Field experiments have been conducted, involving one or multiple factors (Stone 1996, Lambert and McDonald 2017, Schultz and Good 2018). Experimentation is necessary once plausible hypotheses are developed. With any multiple factor phenomenon, such is the case for many eucalypt dieback events, successfully replicating field observations through experimentation is difficult. However, multiple-factor experiments are indeed necessary to determine relationships between factors and tree condition, and have consistently shown encouraging results (Stone et al. 2010, Hossain et al. 2019). These studies have a high potential for understanding eucalypt dieback at the tree scale. While experimentation is often resource-intensive and can have a narrow scope of inference, the strength of the conclusions is high.

#### *Longitudinal experimental studies*

Longitudinal experimental studies track changes to sample units over-time and incorporate multiple experimental treatments. These studies are among the most challenging to complete, and have largely not been undertaken in eucalypt systems. Since some eucalypt diebacks are hypothesized to result from a complex sequence of events (White 1986), involving multiple stressors over-time (Landsberg and Wylie 1983), longitudinal experiments are the only study design capable of proving causation of the process. More commonly, steps in the process are studied individually (Clarke and Schedvin 1999), since these studies are among the most time- and resource-intensive. Worldwide, increasing investment in longitudinal field-based experiments illustrates their importance, particularly in understanding interactions between long-lived trees and climate (Norby and Zak 2011).

### *Retrospective analysis*

The complex spatial and temporal nature of stressors and associated dieback symptoms in eucalypts, combined with a lack of forest surveillance and resources, means that some eucalypt diebacks have been studied retrospectively, after the cessation of dieback (Archibald et al. 2005, Li et al. 2018b). Additionally, retrospective analyses have been used to assess eucalypt recovery from dieback (Moxham et al. 2018). Retrospective analyses can take many forms, and incorporate a variety of data sources. These analyses leverage historical information in an attempt to piece together events and develop plausible hypotheses of the causes of dieback or recovery (Moxham et al. 2018). Retrospective studies suffer from a poor ability to identify biological causal stressors such as insects and pathogens, since many species can act opportunistically on stressed, dying, or dead tissues (Old et al. 1990, White 2015a). However, they may be used to more accurately identify associated physical (landscape position and soils) and physiological factors (Li et al. 2018b). Additionally, where sufficiently accurate monitoring data is available, climate and hydrological factors may be found associated with eucalypt dieback (Moxham et al. 2018). In the future study of eucalypt dieback, retrospective analyses are inevitably going to occur, since they can represent the only option in certain cases. It is important, however, to acknowledge that they lack the ability to discern the role of biological stressors and cannot consider dynamic factors not represented by monitoring data, and therefore is unlikely to provide a complete explanation of the dieback or recovery processes when biotic agents are involved.

### *Modelling studies*

Models represent an important tool for examining relationships between environmental stressors on tree growth and mortality (Gustafson et al. 2015). Some attempts have been made to parameterize models that describe eucalypt response to single stressors, including fire (Strasser et al. 1996) and drought (Medlyn et al. 2007). In the plantation setting, simulation models have been developed and used to predict eucalypt growth (Battaglia et al. 2004, Mummery and Battaglia 2004, Paul et al. 2008), including the well-known 3PG model (Landsberg and Waring 1997). Simulation

modelling, however, has largely not been used in the study of eucalypt dieback, decline, and tree mortality in natural ecosystems. Elsewhere, tree- and landscape-scale models are regularly used to examine the future impact of single, and multiple interacting stressors under climate change and management practices on tree and forest condition (Gustafson et al. 2015). Phenomena such as drought- and fire-induced eucalypt dieback are well-suited for landscape simulation modelling studies (Earles et al. 2014). However, their use is likely limited in Australia by the absence of necessary disturbance effects data, measured from field studies. Simulation models should be explored further for their use in answering critical questions concerning current and future dieback events.

#### *Meta-analysis and review studies*

While there has not been a comprehensive review of the scientific literature or systematic meta-analysis of the available data regarding all types of eucalypt dieback, multiple papers have synthesized portions of the literature base or detail key dieback events (Reid and Landsberg 2000, Close and Davidson 2004, Wardell-Johnson and Lynch 2005, Wardell-Johnson et al. 2005), including reviews of rural tree decline (Reid and Landsberg 2000, Close and Davidson 2004) and Bell-miner dieback (Wardell-Johnson et al. 2005). In certain cases, researchers have attempted to link multiple events across space and time to develop general commonalities between events (Close et al. 2009). Since these comparisons are not systematic examinations, they suffer from low strength of association. Also, in some cases, researchers have selected one or few factors to focus on (Jurskis and Turner 2002, Jurskis 2005b), and since other potential causal factors are not fully reviewed, these studies have limited potential for comprehensively explaining eucalypt dieback events. However, reviews and meta-analyses can generate interesting hypotheses (Close and Davidson 2004), that can later be examined more thoroughly. Reviews and meta-analyses are particularly valuable when there is a substantial base of observational and experimental studies to draw conclusions from, and are much less effective when these foundation studies are lacking.

## Proposed primary causes of eucalypt dieback

A number of primary causes of eucalypt dieback are highlighted by the literature, which we have reviewed below. The challenge in this type of review is that some causes, or topics, gain more research effort than others, partially dependent on the composition of expertise in the different regions, and some are mainly reported on in the grey literature. After an extensive literature search, the primary causes of eucalypt dieback that are most commonly associated with widespread and severe dieback events in NSW and surrounding states are: fire, drought, waterlogging, nutrient disorders, land-use and management, and leaf-feeding insects. A variety of other factors, which we deem as important, either because they cause severe dieback in other regions or may become

important to southeastern Australia in the future are: fungal foliar pathogens, shoot and stem pathogens, root pathogens, mycorrhizal associations, and frost, and are discussed briefly. It is important to note, that some of causes are difficult to put in a particular section, as they are interrelated and complex.

## Fire

### *a. Hypothesized mechanism*

*(see land management section for discussion of prescribed burning)*

Fire can directly damage eucalypts by killing leaves, shoots, girdling branches, stems, and damaging roots (McCaw et al. 1994, Bennett et al. 2016, Prior et al. 2016). Direct fire effects vary considerably from minor leaf scorch, and shoot death (Wardell-Johnson 2000) to tree mortality (Etchells et al. 2020). Many factors contribute to the severity of fire-induced dieback, including but not limited to species attributes, growth stage, canopy height, surrounding vegetation, fire intensity, and time of year, among others (McCaw et al. 1997, Denham et al. 2016, Miller et al. 2019). Eucalypt communities dominated by resprouters are generally tolerant of severe fire (Denham et al. 2016), and assumed to recover quickly post-fire (Gill 1978, Heath et al. 2016). However, results from more recent studies are challenging this assumption, finding that dieback from fire can persist in some eucalypt canopies for many years or decades (Wardell-Johnson et al. 2017, Karna et al. 2019). Legacies of past dieback, including the presence of stagheads or dead grey branches and altered architecture from resprouting, may confuse and cause misleading results in retrospective analyses. Therefore, documenting when and where fire-induced dieback occurred is critical for discerning proximate and ultimate causes of eucalypt dieback, especially in landscape-level analyses. The severity of wildfire in southeastern Australia is projected to increase in the coming decades from climate change, and the extremity of the recent bushfire season has been attributed to combined effects of increasing temperatures and drought (Nolan et al. 2020) with 21% of Australia's temperature broad-leaved and mixed forests having burned, an unprecedented value for any continent in recorded history (Boer et al. 2020). Inevitably, this change will increase the severity of fire-induced dieback, in even the most resilient eucalypt species (Prior et al. 2016).

The frequency and severity of fire disturbance is an important determinant in whether resprouting eucalypts recover from fire-induced dieback or experience progressive crown decline (Fairman et al. 2017). Wildfire frequency, and frequency of large, severe fires are increasing across Australia, including temperature regions of southeastern Australia, and this trend is expected to continue, driven by increased temperatures and drought from climate change (Bradstock 2010, Dutta et al. 2016, Clarke and Evans 2019). In addition, severe wildfire events increase the probability of subsequent events, representing a positive feedback cycle (Barker and Price 2018). Recent studies have found that short-interval, high-severity wildfire increase dieback severity and reduce the

probability of survival in eucalypts by eroding resprouting success (Fairman et al. 2017). Epicormic resprouting, a common response of dry-sclerophyll eucalypts to fire, uses more carbon reserves than basal resprouting (Smith et al. 2018). Indeed, Croft et al. (2007) found that repeated fires deplete carbon resources leading to reduced regenerative capacity. As with fire severity, increasing temperatures and drought in the coming decades is expected to continue current trends in the frequency of severe wildfires and fire-induced dieback events.

Fire can interact with other important stressors to cause eucalypt dieback, particularly drought and heatwaves. One of the primary drivers of high-intensity wildfire is low fuel moisture, which results from a period of low precipitation and high temperatures (Nolan et al. 2016). Both live and dead fuel moisture can reach critically low fuel moistures rapidly during intense drought and heat conditions (Nolan et al. 2016). Extreme high temperatures (i.e. heatwaves) and low relative humidity drive explosive fire growth by effectively ‘pre-heating’ fuels in advance of ignition. This is supported by the fact that wildfires that burn during extreme fire weather (high temperatures, low humidity, and high winds) and drought conditions nearly completely cover the burned area, leaving few unburnt patches (Collins et al. 2019). These stressors, drought, heatwaves, and fire, when combined cause mega-fires (Stephens et al. 2014, Nolan et al. 2020), which results in widespread and severe fire-induced eucalypt dieback. Drought and heatwaves can also interact with fire indirectly, by triggering eucalypt dieback preceding fire (Matusick et al. 2013). In southwestern Australia, patches of eucalypt dieback and tree mortality led to significant alterations to fuel patterns, and models suggest the altered fuel structure can aggravate future fire intensity (Ruthrof et al. 2016). Shifting climate envelopes are expected to leave many carbon-rich forests in southeastern Australia susceptible to drought-induced dieback, which may predispose forests to severe fire-induced dieback (i.e. compound disturbance).

*b. Primary researchers, institutions and seminal outputs*

Ross Bradstock (University of Wollongong) is the Director of the Centre for Environmental Risk Management of Bushfires, and is one of the leading wildfire researchers in Australia. Rachel Nolan (Western Sydney University) has conducted a wide-variety of impactful wildfire research studies, including on the drivers and ecosystem-scale effects. Matthias Boer (Western Sydney University) has an extensive record of publishing on fire in Australian ecosystems using methods ranging from plot-level measurements to remotely-sensed landscape analyses. Craig Nitschke (University of Melbourne) has examined a wide-range of questions regarding forest ecology, including those pertaining to drought and wildfire disturbance in southeastern eucalypts, using a range of study types including landscape ecological models.

*c. The areas of contention and concerns raised with the causal process*

The direct effects of fire on eucalypts is without major contention.

*d. Evaluate and categorize as either likely ultimate or proximate cause of dieback*

Fire is a clear primary cause of dieback in eucalypts, acting directly to damage trees.

*e. Discuss proposed areas of research and potential value of investing in them*

Given the potential for fire-induced eucalypt dieback to reshape ecosystems and affect ecosystem services, we suggest a range of studies are necessary to understand fire-induced eucalypt dieback now and in the future. First, some models have attempted to examine future fire behaviour and effects under climate change in Australia (Matthews et al. 2012). However, it seems clear that there is insufficient empirical data on how different species of eucalypt respond to severe wildfire to accurately predict the extent and severity of tree dieback, and the fuel feedbacks that occur following dieback. We suggest investment in fire effects studies, including traditional cultural burning regimes, that fuse field-based plots with remote sensing and are able to span stand- to landscape-scale in order to develop empirical relationships to improve future predictions. Investigators with historic data and who are able to examine the impacts of the 2019-2020 with field and remote sensing offer particularly strong inference. Further, model ecosystems with differing species, response patterns, and climatic envelopes (i.e. dry to wet and with varying summer extremes) should be targeted for study in order to extend the findings as much as possible, and where possible leveraging previous data with post-fire monitoring following the 2019-2020 fire season. Second, understanding the relative resistance and resilience among co-occurring species is necessary to accurately model fire effects under future climates. Systematic observational field studies are necessary to understand the resistance and resilience (recovery) potential in co-occurring species in forest and woodland ecosystems. Third, compounding disturbance effects are an understudied phenomenon in eucalypt-dominated ecosystems. The bushfire season of 2019-2020 is a case in point where drought and heatwaves coincided with fire to drive extreme fire behaviour and extent. Coastal bushfire impacted areas were then impacted by extreme precipitation in January-February with uncertain consequences to date. Such coinciding events underscores both the complexity of studying dieback as well as the need to integrate multiple data sources, including field-based work, landscape-scale remote sensing and subsequent experimentation, which offers confirmatory evidence of proposed mechanisms. Thus, investment in research activities that span empirical work, experimental work, and simulation modelling to forecast medium and long-term future vulnerability (species, ecosystems, locations) is warranted.

## Drought and heat waves

*a. Hypothesized mechanism*

The responses of plants to extreme events associated with climate change has often focused on drought, or water stress, alone (Allen and Breshears 1998). However, research has recently

progressed to consider “hotter drought” (or “global-change-type drought”) where drought is expected to occur under warmer conditions as global temperatures increase (Breshears et al. 2005, Allen et al. 2015)). This type of hotter drought is causing dieback events in forest and woodland ecosystems worldwide (Allen et al. 2010, Allen et al. 2015, Hartmann et al. 2018). In addition, drought, and heat stress can interact with other disturbances such as fire and windthrow (Brando et al. 2014) and amplify biological disturbances such as outbreaks of damaging insects and pathogens (Williams et al. 2013). Apparent increases in the prevalence of drought and heat-induced dieback as a consequence of recent climate change has sparked a proliferation of research, and interest by land managers observing failing forest and woodland health in many regions of the world (Cobb et al. 2017, Hartmann et al. 2018). Widespread and severe dieback, triggered by water stress, is reshaping ecosystems, shifting species distributions, and threatening the ecosystem goods and services and biophysical and biogeographical land-atmosphere processes that are vital to the health of the biosphere. For example, widespread forest dieback from water stress, heat events and associated disturbances has turned large forested regions, including the Amazon Basin, and North America’s Rocky Mountains from carbon sinks to carbon sources (Phillips et al. 2009, Allen et al. 2010, Allen et al. 2015, Anderegg et al. 2015). The potential for drought and heat-induced forest dieback to alter the future of the planet cannot be overstated, as the loss of terrestrial carbon resulting from dieback represents a positive feedback cycle, contributing damaging CO<sub>2</sub> to the atmosphere and enhancing the global warming trend. However, despite recent advances in monitoring, modelling and experiments of the drivers and consequences of tree death from individual tree to ecosystem and global scale, a general mechanistic understanding and realistic predictions of mortality from drought, and hotter drought are still lacking (Hartmann et al. 2018).

Water stress can be caused by insufficient water availability (i.e. drought) or high water demand (i.e. transpiration) driven by atmospheric demand for water and extreme high temperatures. Drought and heat waves are inherently linked, since they work singling or in combination to cause debilitating water stress in eucalypts. The critical role of high temperatures in driving water stress in trees has only recently been highlighted. For this reason, most research linking water stress to eucalypt dieback has historically focused on drought, and the contribution of high temperatures was rarely mentioned. However, given the prevalence of drought and high temperatures co-occurring during the Austral summer, the influence of heat cannot be discounted as a factor in past dieback events due to its’ absence in the literature.

Water stress from drought and heat is an important source of stress in eucalypt-dominated ecosystems throughout Australia, and can directly cause eucalypt dieback in absence of other sources of stress (Pook et al. 1966, Pook and Forrester 1984, Pook 1985, Ashton and Spalding 2001). Drought-induced eucalypt diebacks have been observed throughout southern Australia, including multiple events in the Canberra region in 1965 (Pook et al. 1966) and 1980s (Landsberg 1985),

repeated deaths on dry mountain slopes in Victoria from the mid-1960s to 1990s (Ashton et al. 1975, Ashton and Spalding 2001), southeastern Tasmania in the early 1980s (Davidson and Reid 1989), and in the upper Murray-Darling basin during the Millennium drought (Horner et al. 2009, Cunningham et al. 2011, Kath et al. 2014, Jensen and Walker 2017, Moxham et al. 2018). In NSW, localised eucalypt dieback events occurred during many minor droughts since the 1860s, and widespread dieback events occurred coinciding with prolonged drought periods, including during the Federation Drought (1895-1903), the drought of 1939-1945, drought in the 1980s (Pook 1985), and the Millennium drought (Semple et al. 2010). Auclair (1993) highlighted extreme drought was associated with dieback of trees throughout the Pacific rim, and outlines the evidence for these events in Australia. Commonly, drought-induced dieback results in premature abscising of leaves and shoots (Pook 1985). However, severe drought-induced dieback can cause complete dieback, tree mortality, and alterations to the structure and composition of eucalypt forests and woodlands (Pook and Forrester 1984, Davidson and Reid 1989, Sanger et al. 2010), making this an ecologically important source of dieback. Instances of drought-induced dieback are expected to increase in the coming decades, due to increased frequency and severity of drought events (Herold et al. 2018). Given reports of drought-induced dieback and mortality (Matusick et al. 2013, Li et al. 2018b) and the projected increases in frequency and severity of drought and heatwave events (Sheffield and Wood 2008, Seneviratne et al. 2014, Trenberth et al. 2014), results in further instances of drought-induced dieback being expected to increase in the coming decades. This is mainly due to most forest species operating with rather narrow hydraulic safety margins against injurious levels of drought stress (Choat et al. 2012).

Drought-induced eucalypt dieback can occur through hydraulic failure: when the supply of water falls to a critically low level, fails to reach the necessary tissues, and xylem cavitation (embolism) occurs (Li et al. 2018a, Blackman et al. 2019). Extended droughts may cause substantial depletion of carbohydrate reserves (Adams et al. 2017), which is thought to also lead to drought-induced dieback in certain species (Kono et al. 2019), though this has yet to be shown in eucalypts (Mitchell et al. 2013). Given that chronic stressors such as temperature and moisture changes are predicted to increase, but also the acute stressors of heatwaves and sudden and severe droughts, it is critical to understand how different eucalypt species will respond, from leaf-level physiological mechanisms, to ecosystem level and implications for water and carbon dynamics.

Some site and stand factors most commonly associated with drought-induced dieback are shallow soils with low water-holding capacity (Jones et al. 1990, Ashton and Spalding 2001), high competition (Horner et al. 2009, Matusick et al. 2013), exposed topographic locations (Ashton and Spalding 2001, Brouwers et al. 2013, Andrew et al. 2016), and areas high in the landscape and disconnected from potential groundwater (Ashton and Spalding 2001, Brouwers et al. 2013). In the ACT and surrounding tablelands in March 1965, for example, wilting and death of dry sclerophyll

eucalypts were widespread, and was most rapid in stands on shallow skeletal soils and slopes of northwesterly aspect (Pook 1981). These site and stand associations have an effect on the supply, storage, and atmospheric demand for water.

While drought can act alone to cause eucalypt dieback, more commonly drought is implicated along with other stress factors (Landsberg and Wylie 1983, White 1986, Keith et al. 2012). Indeed, drought seems to be the most common stress factor associated with more complex eucalypt diebacks, making it one of the most important contributors to eucalypt dieback in southern Australia. Evidence suggests it can interact with other climatic, hydrologic, fire-associated, and biological stress factors in multiple ways leading to eucalypt dieback. For example, and has been mentioned, drought commonly co-occurs with heat-waves during Austral summers (i.e. climate change-type drought) (Mitchell et al. 2012, Ruthrof et al. 2018) and can cause sudden and severe water stress (Bader et al. 2014, Li et al. 2018b). Increasing temperatures exacerbates drought by further depleting soil water (Cai et al. 2009). In the Murray-Darling basin, rising temperatures have caused a 45% reduction in soil moisture (Cai et al. 2009). The combination of drought and heat-induced water stress has led to extensive cavitation, severe dieback and tree mortality in the ACT and Monaro Region in 1965, southwestern Australia in 2010-11 and *E. piperita* in NSW in 2017 (Li et al. 2018b). The combination of drought and modified flooding regimes has caused soil salinization and associated eucalypt dieback in the Murray-Darling basin (Slavich et al. 1999). Modelling studies suggest that salinized groundwater exacerbates the effects of drought in these floodplain ecosystems (Kath et al. 2015). However, repeated stress events can also cause a gradual process of dieback with periods of recovery between, which often allows trees to regain some health, but also, potentially create opportunities for pathogens and insect outbreaks, producing a tree decline recovery seesaw (Whyte et al. 2016). Research in this area of complex interactions between drought and other factors is limited.

The combination of drought and biological stressors, including many insect pests (Keith et al. 2012, Wills and Farr 2017) and certain fungal pathogens (Old et al. 1990) leads eucalypt dieback. Drought can trigger outbreaks of woodboring beetles (Mattson and Haack 1987), which combined have caused extensive dieback in certain locations, including several *Eucalyptus* species in the Canberra area (Pook et al. 1966) and on specific sites in *E. marginata* forest (Seaton et al. 2015) in southwestern Australia. Some evidence of simple positive associations between drought and leaf-feeding insects exist on eucalypts (Keith et al. 2012, Ross 2014, Wills and Farr 2017). However, White (1969) proposed a more complex interaction, including waterlogging stress during wet winters followed by summer drought predisposing trees to attack by leaf-feeding insects. This hypothesis has been supported by others instances of observed dieback, as outlined in the review by Collett (2001). For example, Landsberg and Wylie (1983) found a similar pattern of climate factors preceded dieback of rural trees in southern Queensland. Hossain (2019) found that a similar sequence of events (drought followed by well-watering) increased the development of a canker pathogen contributing to

extensive dieback in *Corymbia calophylla*. It remains unclear how much eucalypt dieback can be explained by the interaction between drought and biological stressors. In an analysis by Mitchell (2014) approximately 50% of their case-studies of drought-induced eucalypt dieback also involved insect pests. The collection of studies documenting the interaction highlights the importance of drought timing, and the sequence of multiple stressors, as a critical factor in causing eucalypt dieback.

*b. Primary researchers, institutions and seminal outputs*

A wide-variety of physiologists and ecologists have been examining the underlying mechanisms of how eucalypts resist and recover from drought at multiple spatial scales through observational and experiment-based studies. These include, primarily Brenden Choat, Sebastian Pfautsch, Melanie Zeppell, and Belinda Medlyn at Western Sydney University. Chris Blackman (Macquarie University) and Tim Brodribb (University of Tasmania) have also been integral to our contemporary understanding of how drought affects eucalypts at the plant-scale. Patrick Mitchell (CSIRO), Anthony O'Grady (CSIRO), and Craig Nitschke (University of Melbourne) have made large advancements in understanding the relationships between drought events at the site and stand scales, including common attributes and drivers. Rod Fensham (University of Queensland) has helped understand drought-induced dieback in Queensland, and has explored the historical, ecological and physiological processes driving native plant abundance.

*c. The areas of contention and concerns raised with the causal process*

Drought alone, causing critically low water availability to trees, as a singular cause of dieback may occur, particularly on sites with low-water holding capacity, and seems not to be in contention. However, the recent realization that high temperatures exacerbates drought effects (transpirational demand increases exponentially with temperature), the high frequency in which the two stressors co-occur, and the difficulty in disentangling their respective roles in any given situation means that many future observations are likely to be attributed to the combination heat and drought stress when they co-occur. While drought acting singly, or in combination with high temperatures, appears clear in the absence of other stressors, when biological stressors are also present the causes of diebacks are commonly in debate. In the absence of a consistent generalized interactive mechanism between drought and biological stress agents (e.g. hypothesis proposed by White (1969), these debates are likely to continue. This may especially be true when neither stress agent (drought or biologicals) are of sufficient intensity to cause dieback alone.

*d. Evaluate and categorize as either likely ultimate or proximate cause of dieback*

Since most moisture-related tree stress originates from drought and heat in Australia, and its incidence and severity are independent from other stressors, it should be considered a primary cause of dieback.

e. *Discuss proposed areas of research and potential value of investing in them*

Given the projected future climate of southern Australia, including expected increased prevalence of drought (a combination of increased dry periods and elevated plant water demand due to uniformly elevated temperatures), we believe that there is significant value in continued investment into this stressor. Specifically, we have highlighted four avenues of research that are particularly important to predicting when and where drought-induced eucalypt dieback is likely to occur, which is of importance to land managers. First, there is significant value in investing in efforts to understand the mechanisms by which drought and moisture stress cause dieback. These include studies that seek to fundamentally understand which species and attributes are capable of *resisting* and *recovering* from water stress, since both are vitally important for predicting ultimate effects (i.e. species and trait-based physiological research). Second, systematic efforts to detect and document drought-induced dieback are limited, leading to a disconnect between field observations of dieback and specialist-directed measurement of mechanistic drivers and plant-level effects (i.e. plant water status). Future predictive ability is predicated on the feedback from observations of eucalypt dieback in the field. Therefore, investment in systematic forest and woodland surveillance systems (e.g. remote sensing), and the processes that allow for follow-up site investigations would be prudent (i.e. observational research). Third, there is evidence that basic observations of drought-induced dieback may have been taken for granted in the past, due to their obvious cause (Semple et al. 2010), or due to a greater focus on proximate causes of dieback (Reid and Landsberg 2000). Thus, retrospective analyses should be undertaken that target eucalypt species that have been plagued by complex dieback events, and where drought has been suspected as a causal factor. Exploring the ability of dendrochronological techniques and historical remote-sensed data sources to identify patterns of stress will be critical to developing accurate models (i.e. retrospective research). Fourth, investment in research studying the interactive effects of drought and other stress factors is also critical, given the frequency with which it has occurred. More specifically, a systematic, well-replicated testing of the hypothesis first outlined by White (1969), and which has garnered support from observations since (Landsberg and Wylie 1983, Collett 2001), would help to conclusively determine whether it represents a consistent generalized mechanism that can be planned for and leveraged in the development of predictive tools.

## Waterlogging

a. *Hypothesized mechanism*

Many eucalypt species are intolerant of waterlogging stress (Ladiges and Kelso 1977), which can directly cause root hypoxia (Burgess et al. 1999) and the development of irreversible tyloses in xylem vessels (Davison and Tay 1985), blocking water transport in the tree and inducing ‘physiological drought’ (water stress despite sufficient water availability). Additionally, waterlogging

can induce nutrient deficiencies and decrease photosynthesis rate and phytochemical efficiency (Close and Davidson 2003). In mature trees, crown symptoms may be consistent with those associated with drought, including rapid loss of leaf, shoot, root and stem dieback (Bond 1945, Matusick et al. 2016a). Prolonged waterlogging leads to tree mortality; more commonly, however, waterlogging is seasonal in temperate and Mediterranean climates (White 1969), meaning trees experience acute waterlogging followed by seasonal relief. Sites susceptible to waterlogging includes water-gaining sites in valleys (Cramer et al. 2004) and those with impermeable subsurface soil substrates (White 1969). Many historical eucalypt dieback events have patterns consistent with waterlogging stress, including a wide variety of leaf-feeding insect outbreaks (leading to dieback) in southeastern Australia (White 1969), Ourimbah Dieback near Gosford, NSW, Gully Dieback in Tasmania (Bird et al. 1974), dieback of mixed-eucalypt forests in eastern Victoria (Marks et al. 1972), and Jarrah Dieback in southwestern Australia (Davison 2014). In contrast to these scenarios, eucalypts dominating floodplains have developed mechanisms for maintaining healthy tissues in the presence of hypoxic conditions (Blake and Reid 1981, Akilan et al. 1997). Most waterlogged soils outside of floodplain forests develop after intensive clearing or thinning of deep-rooted native vegetation, and subsequent rising water tables (Davison 2015).

Most frequently, waterlogging stress is associated with salinization stress (Froend et al. 1987, Barrett-Lennard 2003), since rising water tables mobilize salts which have been historically stored in unsaturated portions of the profile (Jolly et al. 1993, Bell 1999, Cramer and Hobbs 2002). Two circumstances where this combination of stressors regularly occurs are in semi-arid regions where clearing of native vegetation has increased secondary salinization (Seddon et al. 2007, Macinnis-Ng et al. 2016), and semi-arid floodplain forests in NSW and South Australia where hydraulic changes have decreased flood frequency and increased salinized water tables (Jolly et al. 1993, Horner et al. 2009, Kath et al. 2015). High sodium ( $\text{Na}^+$ ) and chloride ( $\text{Cl}^-$ ) concentrations in stems, shoots, and leaves (Adams et al. 2005), which, in turn, interferes with water transport by disrupting natural osmotic gradients (Cha-um and Kirdmanee 2010). Scenarios where salinization and waterlogging cause eucalypt dieback are associated with significant land-use changes. For example, in the lower Murray-Darling basin where dieback of *E. camaldulensis* and *E. largiflorens* have been well documented (Jolly et al. 1993, Overton et al. 2006, Cunningham et al. 2011), rising water tables and salt concentrations have been attributed to changes in flood regimes sparked by river regulation in the 1920s (Jensen and Walker 2017). Drought may exacerbate this phenomenon by further reducing the frequency of regulated water releases from dams and restricting the surface-water available for floodplain trees (Leblanc et al. 2012). Eucalypt dieback is also common in semi-arid rural regions where extensive clearing of native vegetation for the expansion of agricultural lands have altered subsurface hydrology (Froend et al. 1987, Cramer and Hobbs 2002, Seddon et al. 2007) and caused secondary salinization. “Dryland salinity” is considered a major risk to many threatened species in NSW (Zeppel et al. 2003). In the South West Slopes area of NSW, Seddon (2007) estimated that 14%

of riparian forests and 6% of yellow box-Blakely's red gum woodland exhibited signs of degradation from salinity and waterlogging. It is unclear whether widespread eucalypt dieback from the combined effects of salinization and waterlogging would occur in the absence of these landscape-level land-use changes. Regardless, the amount of area affected by this condition is significant, and the combination of waterlogging and salinization stress is likely to continue to affect eucalypts in fragmented landscapes.

Waterlogging stress can also interact with biotic stressors, by predisposing attack. For example, several periods of high rainfall in the 1950s are thought to have predisposed Sydney blue gum on sites prone to waterlogging to attack by psyllids and woodboring beetles (Moore 1959). Stone (2010) found that the lerp-forming psyllid *Creiis lituratus* preferentially defoliated *E. dunnii* trees experiencing waterlogging stress in northeastern NSW. Similarly, high rainfall and waterlogging of certain microsites preceded a more recent outbreak of *Cardiaspina* spp. in grey box dry woodlands west of Sydney, NSW (Hall et al. 2015). Root disease caused by *Phytophthora* species, particularly *P. cinnamomi*, requires adequate soil moisture for infection and disease development. Waterlogging, and associated root hypoxia, increases the susceptibility of roots and stems to infestation (Burgess et al. 1999) and the combination of waterlogging and *P. cinnamomi* is thought to explain dieback of *E. marginata* on many sites in southwestern Australia (Davison 2018).

*b. Primary researchers, institutions and seminal outputs*

Most recently, floodplain forests have been studied extensively for their relationships between tree health and waterlogging and salinity stress. Some researchers that have examined these relationships using a variety of methods, including modelling studies and observations studies with longitudinal designs, include Shaun Cunningham (Deakin University) and Jarrod Kath (University of Southern Queensland). Mark Adams (Swinburn University of Technology) has conducted physiological studies on the effects of these stressors on plants. Christine Stone (NSW Department of Primary Industries) and Markus Riegler (University of Western Sydney) have made critical observations and drawn relationships between these abiotic stressors and leaf-feeding insect outbreaks.

*c. The areas of contention and concerns raised with the causal process*

The relationship between salinity, waterlogging, and vegetation response is well described. Recognizing the environmental benefits of maintaining near natural flood regimes, and hence additional environmental water releases from dams in the Murray-Darling basin since the 1990s (Leblanc et al. 2012) have contributed to an improvement in tree health (Souter et al. 2014). However, some debate exists surrounding the relative role of salinity and waterlogging in the dieback of rural eucalypts. It is also unclear how climate change will affect water tables in the future. While expectations of decreased precipitation may make these stressors less important, an increased

frequency of high rainfall events may exacerbate the problem in rural regions. Also, it is unclear whether widespread and severe tree mortality has the potential to alter water table depth and waterlogging occurrence.

*d. Evaluate and categorize as either likely ultimate or proximate cause of dieback*

Given the strong association between salinization, waterlogging, and landscape-scale land-use changes, we would consider these instances of eucalypt dieback proximate causes. In the absence of widespread clearing in rural regions and flood control in semi-arid floodplain forests, there is limited evidence that widespread dieback would occur.

*e. Discuss proposed areas of research and potential value of investing in them*

The combination of salinization and waterlogging stress is likely to continue in the outlined circumstances. In floodplain ecosystems, these stressors are expected to be exacerbated by high temperatures (increased water demand but elevated soil water salinity) (Cai et al. 2009) and drought (decreasing frequency of flood events) (Kath et al. 2015). Modelling studies in the last decade have explored the water availability necessary to maintain tree health in floodplains, incorporating both expected climate changes and project human water needs (Cunningham et al. 2011, Catelotti et al. 2015). However, these studies should be expanded and updated regularly in an effort to predict the needs of floodplain ecosystems and maintenance of tree and forest health. The mechanisms causing eucalypt dieback in semi-arid floodplain forests and rural landscapes affected by secondary salinity are relatively clear. For upland areas experiencing waterlogging due to land use change and altered climate, future research quantifying relative susceptibility particularly at the trait level (rooting pattern, wood density, etc) would be helpful to understand risk and inform management. What remains unclear is how climate change, particularly the impacts of rising average temperatures and the increasing frequency of heatwaves and extreme droughts have on groundwater levels and the combined effects of waterlogging and salinization on trees. In order to accurately model these effects under future climate scenarios, empirical relationships must be determined between these climatic and hydrological factors.

## Leaf-feeding Insects

*a. Hypothesized mechanism*

Leaf-feeding insects represent an important and widespread stress agent in eucalypt forests and woodlands (Landsberg and Cork 1997). These insects generally fall into multiple feeding guilds, including leaf mining, chewing, skeletonizing, and sap-sucking (Abbott et al. 1993, Stone et al. 1998). The most common groups of leaf-feeding insect pest of eucalypts include psyllids (Hemiptera: Psyllidae), chrysomelid leaf beetles (Coleoptera: Chrysomelidae), scarab beetles (Coleoptera:

Scarabaeidae), and weevils (Coleoptera; Curculionidae), among others. Leaf-feeding insects cause damage ranging from small, scattered spots of necrosis on affected leaves to severe defoliation in mature trees (Lowman and Heatwole 1992). A single defoliation event is unlikely to cause severe eucalypt dieback (Landsberg and Cork 1997). Rather, repeated and severe defoliation over multiple seasons and years can result in significant crown loss and dieback (Lowman and Heatwole 1992).

Outbreaks of leaf-feeding insects, leading to dieback, have been reported in ecosystems throughout southern Australia. The most well-known diebacks associated with leaf-feeding insects are rural diebacks of eucalypts (Landsberg 1988), including New England dieback in the Tablelands region of NSW (White 1969, Mackay et al. 1984). However, leaf-feeding insects are associated with many other dieback events, including Bell-miner dieback of eucalypts in northeastern NSW and southern Queensland, which can occur in fragmented or intact communities (Wardell-Johnson et al. 2005), dieback of *E. moluccana* west of Sydney, NSW (Hall et al. 2015), *E. blakelyi* in the southern Tablelands of NSW and Victoria (Clark 1962), *E. camaldulensis* (Stone and Bacon 1994, Collett 2001), dry sclerophyll forests in Tasmania (Elliott et al. 1981), *E. rudis* (Clay and Majer 2001), *E. marginata* (Strelein 1988) and *E. occidentalis* (Farr 2019) in southwestern Australia, among many others. The consistency with which leaf-feeding insects are associated with eucalypt diebacks highlights their importance as sources of stress in the region.

A combination of top-down and bottom-up factors regulate leaf-feeding insect populations (Stone 2005, Steinbauer et al. 2015) (Figure 3), which can reproduce rapidly if allowed. Top-down regulating factors are agents that directly kill or predate upon leaf-feeding insect pests, and include extreme temperatures (Angel et al. 2008), leaf-gleaning birds (Haythorpe and McDonald 2010), and parasitoids (Steinbauer et al. 2015) in Australia. Bottom-up regulation refers to the quality of food resources (Ohmart et al. 1985), which controls the growth-rate and fecundity of the insect pests. These generally include the abundance, nutrient and water content of leaves (Steinbauer et al. 2015). Bottom-up and top-down regulating factors can, in turn, be directly or indirectly (through tree stress) affected by weather and edaphic factors, and land-use or management, creating a complex web of interactions. Additionally, these interactions are species/system-specific, making it exceedingly difficult to draw generalizations (Duursma 2016, Hoffmann et al. 2019). When one or more of regulating mechanisms are relieved or absent, leaf-feeding insect outbreaks can occur (Figure 3). The length of the time regulating mechanisms are absent, or whether both top-down and bottom-up regulators are absent may determine the length of the outbreak (White 1966). For example, in eucalypt forests and woodlands west of Sydney, outbreaks of a *Cardiaspina* psyllid species can intensify during warm winters (Hall et al. 2015), and populations can crash dramatically during acute summer heatwaves when eucalypt foliage becomes unpalatable (Hall et al. 2015, Duursma 2016). Severe dieback events, most closely-associated with leaf-feeding insects, are thought to result from extended outbreaks, enabled by a protracted period in the absence of regulating mechanisms (Landsberg 1990b). When eucalypts dieback and resprout epicormically, resprout foliage is more

attractive and more nutritious to some leaf-feeding insects (Landsberg 1990a, Marsh and Adams 1995, Steinbauer et al. 1998, Thomson et al. 2001, Steinbauer et al. 2015). This process of dieback, epicormic resprouting and increasing infestation intensity represents a positive feedback cycle (runaway outbreaks) (Figure 4) (Craig 2010), whereby leaf-feeding insect populations can increase quickly corresponding with multiple dieback and resprout episodes. In the absence of appropriate feedbacks, where neither top-down and bottom-up regulators control insect pest populations, repeated dieback episodes turn into tree decline and often to tree death (Figure 4). Disrupting the dieback-resprout-dieback positive feedback cycle is critical to enabling recovery of dieback-affected eucalypts. For example, several studies have used insecticide and enclosure strategies under experimental conditions to restore regulating mechanisms, lower insect herbivory, and improve tree health (Mackay et al. 1984, Lowman and Heatwole 1987, Stone 1996). When ecosystems are intact, the positive feedback dieback cycle is thought to be interrupted by top-down regulators or by resource depletion. When top-down regulators fail to materialize, and outbreaks continue, it can represent a sign of ecological dysfunction and suggest other factors have destabilized the ecosystem (Florence 2005). Therefore, identification of the top-down and bottom-up regulating factors is a critical first step in diagnosing complex eucalypt dieback involving leaf-feeding insects.

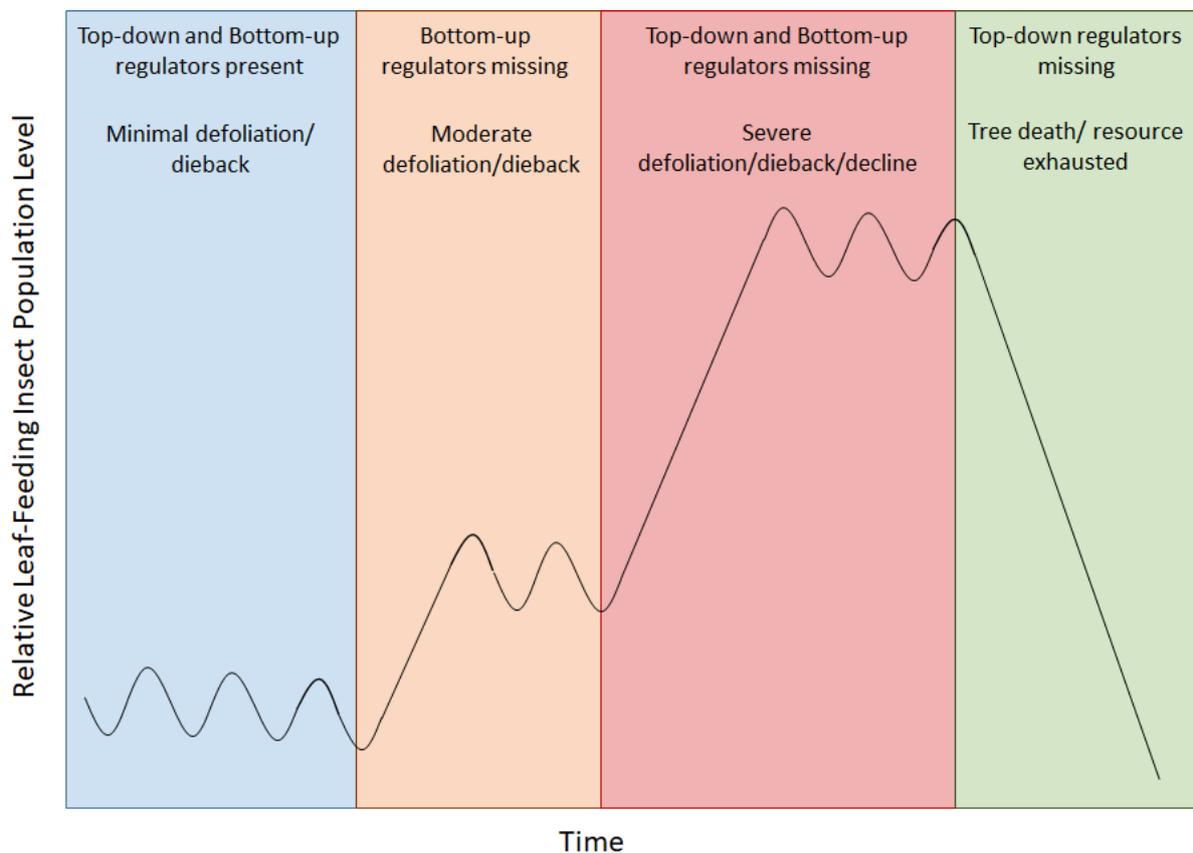


Figure 3. Theoretical relationship between severity of leaf-feeding insect population levels and regulating processes in eucalypts of southern Australia. As bottom-up and top-down regulators

disappear from an ecosystem, outbreak severity may intensify with associated eucalypt dieback reaching severe levels, and in some cases causing tree mortality. Insect populations crash when the resource is extinguished.

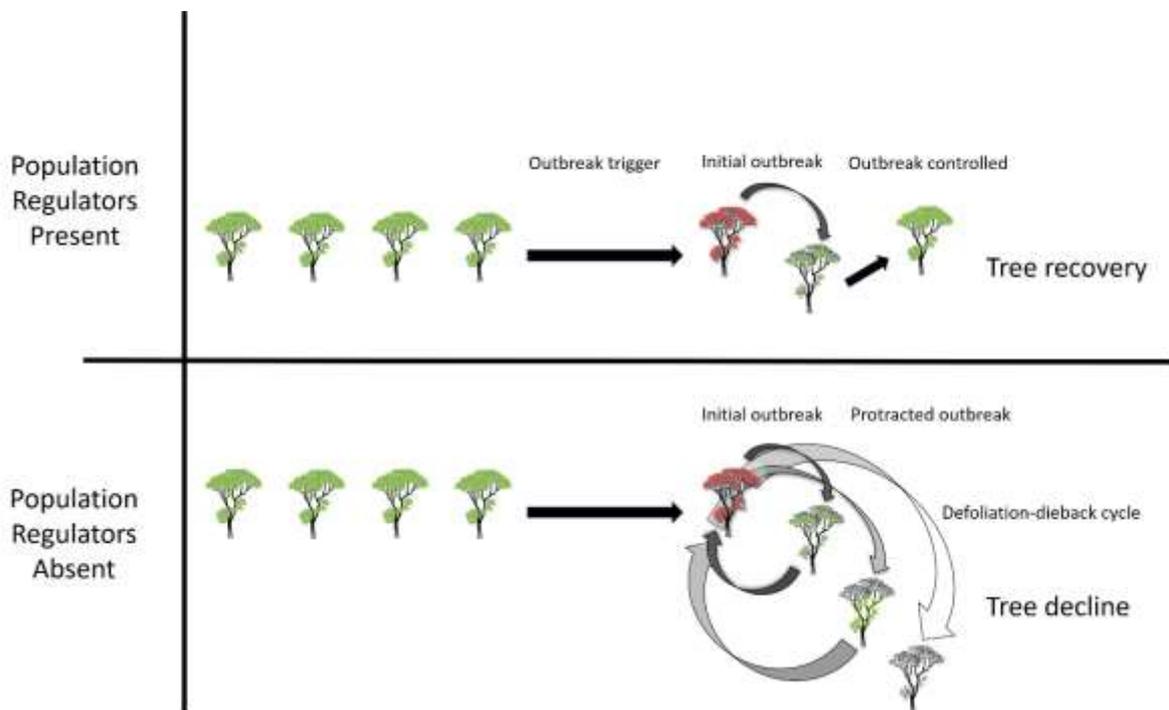


Figure 4. In the presence of population regulators, the initial outbreak of leaf-feeding insects is brief and tree recovery can occur. When regulators are absent, or weak, a positive feedback (defoliation-dieback) cycle can ensue, leading to tree decline and mortality.

Multiple hypotheses have been proposed for how the absence of critical top-down and bottom-up regulating factors have facilitated certain complex leaf-feeding insect-associated diebacks. While studying dieback of *E. fasciculosa* in rural South Australia, White (1969) hypothesized that waterlogging during winter (causing root mortality), followed by summer drought increased the nutrient content of foliage (palatability), and thus insect survival and fecundity. Later White (1986) extended the hypothesis to include New England Dieback in rural NSW. In both cases, White (1969, 1986) hypothesized that a sequence of climate stressors alleviated bottom-up regulating factors, permitting insect populations to reach outbreak levels. In addition, the dieback events occurred in regions subjected to intensive land use and management changes, potentially altering the presence and/or behaviour of top-down regulators (Watson 2002). This hypothesis was supported by observations by (Mackay et al. 1984) in the Tablelands, which found trees on sites prone to waterlogging were most severely affected. Stone (2008) also found that sites most severely affected by Bell-miner dieback in NSW had high Topographic Wetness Index values (most prone to waterlogging). Further, more widespread work also supported White's hypothesis: rural dieback in southern Queensland (Landsberg and Wylie 1983), gumleaf skeletoniser (*Uraba lugens* Walker) in in

Western Australia (Farr et al. 2004), and others throughout eastern Australia (Collett 2001). Finally, Marsh and Adams (1995) have shown that *E. tereticornis* prone to rural dieback in Victoria have higher nutritional content of sap and leaves (bottom-up factor), which increases during drought and propels outbreaks. Climatic changes and land-use and land management practices that increase the susceptibility of trees to drought and heat stress, physiological drought and waterlogged soils, which may trigger outbreaks, and disrupt top-down negative feedback mechanisms on populations, are likely to increase the prevalence of this process. The hypothesis by White (1969), including complex interactions between climatic, nutrient dynamics, and leaf-feeding insects in causing eucalypt dieback, highlights the interdisciplinary and dynamic nature of complex eucalypt dieback events and the need to use appropriate study approaches.

Bell-miner dieback is a similarly complex eucalypt dieback phenomenon, strongly associated with the presence of multiple miner species (birds in the genus *Manorina*, mainly Bell-miner, *Manorina melanophrys*) and leaf-feeding insects (psyllids) (Stone 1996, Stone et al. 2008) (O'Loughlin et al. 2014) in northeastern NSW and southern Queensland. Bell-miner dieback can occur on sites with altered land-use histories (Wardell-Johnson and Lynch 2005), but also occurs in areas with minimal past disturbance (CFOC 2014). Psyllids replicate quickly on new foliage, reaching outbreak levels and facilitating the defoliation-dieback cycle (Keith 2017)2015). The flushes of new growth which trigger outbreaks are varied, and may simply include growth responses to periods of good growing conditions. It is hypothesized that alterations to the dynamics of top-down regulators (leaf-gleaning birds) contribute by reinforcing and prolonging outbreaks (Keith 2015). Specifically, invasion of habitat patches by miners displaces most other bird species (Dare et al. 2007). Bell-miners are less effective top-down regulators than other insectivorous bird species (Kemmerer et al. 2008, Haythorpe and McDonald 2010), and it is hypothesized that this displacement provides the window of opportunity for psyllids to maintain high populations (Stone 1996, Clarke and Schedvin 1999). In other words, continual flushes of new growth and prolonged displacement of top-down regulators are thought to enable repeated defoliation, crown dieback and tree decline. Manipulative studies have generally provided support for the hypothesis. For example, Loyn (1983) and Clarke and Schedvin (1999) removed bell-miners from woodland severely-infested by miners and psyllids, and observed diversification of the bird community and a rapid, significant drop in insect populations. Clarke and Schedvin (1999) and Dare (2007) observed outbreaks of psyllids shortly after the arrival of miners. Bell-miner dieback provides an example the complexity of ecological systems, how leaf-feeding insects take advantage of new foliage, and how relatively slight changes (invasion by a native species) can alter the dynamics necessary to cause eucalypt dieback.

It has also been hypothesized that the invasion of exotic weeds in the understory of eucalypt forest facilitates Bell-miner dieback (Stone et al. 2008). Lantana (*Lantana camara*) has invaded the understory of some coastal forests in eastern Australia, and has been found weakly associated with Bell-miner dieback in northeastern NSW (Stone et al. 2008). Recent research suggests that lantana is

not a causal factor in Bell-miner dieback (Lambert and McDonald 2017), including experimental evidence that removal of lantana fails to change overstory health (Lambert et al. 2017). However, Stone (1999) and Stone et al. (2008) outlined compelling evidence of additional ecological dysfunction due to the presence of lantana and overstory disturbance. Lantana invades forest understories following canopy disturbance (Duggin and Gentle 1998), responding to increased understory light levels. Any disturbance that increases light levels is likely to favour lantana, including fire, grazing and logging (Gentle and Duggin 1997b, Kavanagh and Stanton 2003). Lantana and other dense understory cover provide critical habitat for Bell-miners, enabling their colonization (minimizing top-down regulators) (Pearce and al 1995, Lambert et al. 2016, Lambert and McDonald 2017). In the absence of lantana, partial canopy disturbance can lead to eucalypt regeneration and canopy recovery (Stone et al. 2008) (Figure 4). However, Lantana restricts regeneration by excluding native vegetation (Gentle and Duggin 1997a) and following partial canopy disturbance, lantana responds favourably by increasing understory density (Gentle and Duggin 1997b), thus improving habitat for miners. In conjunction with understory changes, overstory trees can respond to partial canopy thinning by initiating new growth, which is attractive to some psyllids (Gherlenda and al. 2019). In the absence of lantana, the diverse assemblage of top-down avian predators may hasten psyllid outbreaks (i.e. intact ecosystem functioning). In the presence of lantana, bell-miners can establish and reinforce psyllid outbreaks and eucalypt dieback through non-lethal feeding behaviour (Haythorpe and McDonald 2010). The land management history of the northeastern NSW region, including a long history of logging which simultaneously facilitates canopy openings, weed invasion and a growth response by canopy trees, may have provided the necessary ingredients for the trophic cascade postulated by Stone et al. (2008) on certain sites. The ecological dysfunction described (e.g. lantana and Bell-miner relationships) is not, however, adequate to comprehensively explain Bell-miner dieback, since it occurs in areas not subjected to logging disturbance and lantana (CFOC 2014). Therefore, it should not be considered a primary cause of dieback events, but rather a potential reinforcing process on a subset of sites.

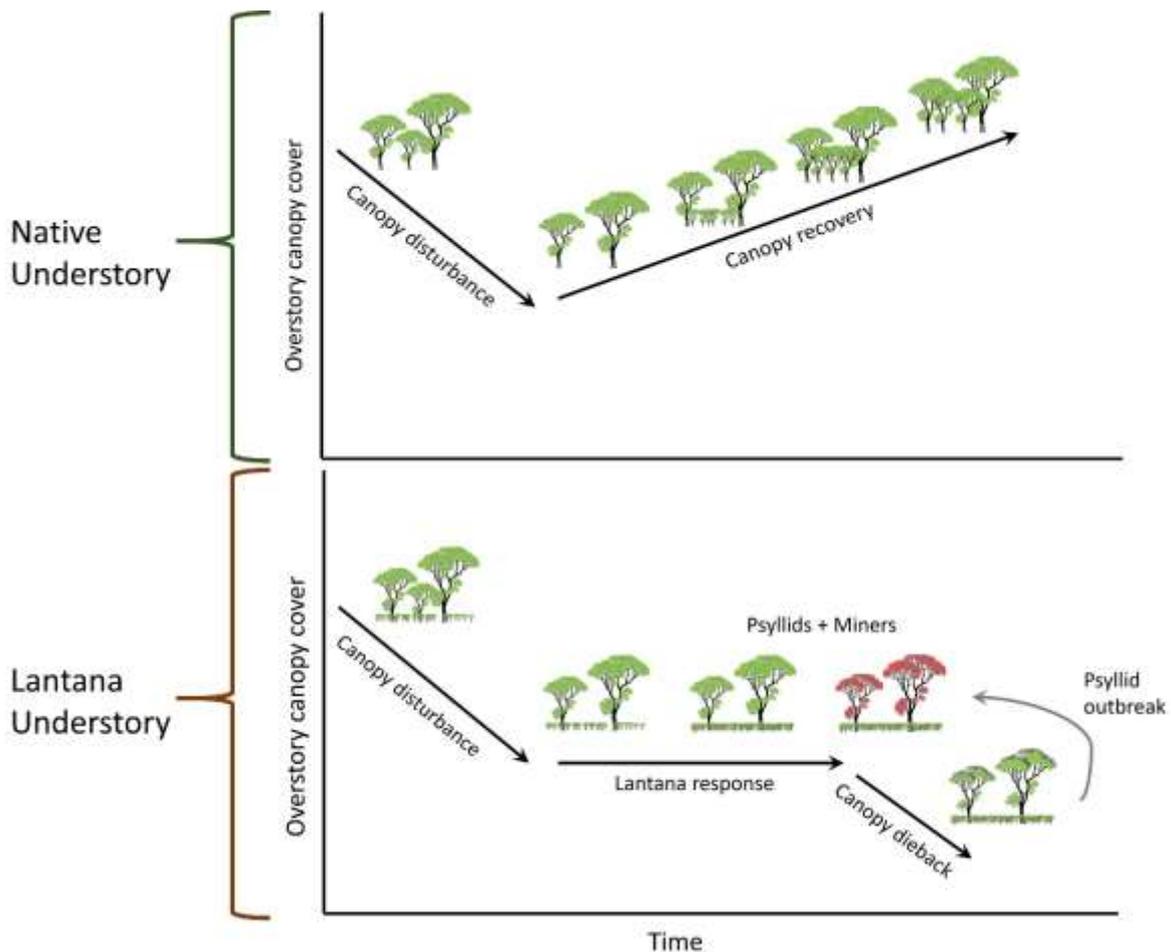


Figure 4. It is hypothesized that in the presence of native understory, eucalypt-dominated ecosystems in northeastern NSW responds to canopy disturbance by recruiting new eucalypts, resulting in a closed eucalypt canopy. However, in the presence of lantana in the understory, regeneration is restricted and lantana density increases, resulting in persistent canopy openings. Canopy openings favour Bell-miner site colonization, which, in turn, may reinforce psyllid pest outbreaks. This trophic cascade represents a positive feedback cycle resulting in eucalypt dieback (Stone 1999, Stone et al. 2008).

*b. Primary researchers, institutions and seminal outputs*

Markus Riegler (University of Western Sydney) and his graduate students have published several recent important papers on the behaviour of psyllids, factors triggering outbreaks, and their impacts on eucalypt dieback near Sydney. Martin Steinbauer (La Trobe University) studies leaf-feeding insects, and contributed important findings to the interactions between psyllids and Bell-miner dieback. Paul McDonald (University of New England) and Nick Reid (University of New England), along with their graduate student Kathryn Lambert (University of New England) have published the some of the most recent research on the relationships between Bell-miner, habitat, and eucalypt dieback. Christine Stone (MSE Department of Primary Industries) is an expert entomologist and

forest health specialist that published research critical to explaining Bell-miner and other eucalypt dieback events involving leaf-feeding insects.

*c. The areas of contention and concerns raised with the causal process*

Much of the contention and uncertainty seems to arise regarding which ultimate causal factors trigger and sustain leaf-feeding insect outbreaks. Conceivably, there is no one factor, but rather a variety of factors (depending on circumstance) that triggers outbreaks (leading to the confusion). The research shows that relationships between leaf-feeding insect species, genera, or guild and host-specific, in many cases. This fact limits the number of generalities that can be drawn from studying a single system. Since certain psyllid genera specialize on new foliage, which can ultimately lead to outbreaks (Gherlenda et al. 2016), any natural growth patterns or disturbances which trigger growth responses (e.g. logging, recovery following fire or drought-induced dieback) may predispose trees to leaf-feeding insect outbreaks and start the defoliation-dieback cycle, especially in the absence of top-down regulators. There is also still contention over the role of lantana, in our view, with regards to its role in Bell-miner dieback (Lambert and McDonald 2017, Lambert et al. 2017). Lambert et al. (2016) made several important advancements to our understanding of lantana, including that Bell-miners are not dependent on it for nesting habitat, it is likely not altering nutrient dynamics, and its removal is not likely to increase tree health alone. However, portions of the hypothesis proposed by Stone and Stone et al. (1999, 2008) have not been fully tested, including the interaction between lantana invasion, overstory disturbance, and maintenance of persistent openings (creating the habitat conditions necessary for Bell-miners to flourish). Understanding these relationships is likely to only explain dieback on a subset of sites, however, where each of the factors (overstory disturbance, lantana, and Bell-miners) co-occur.

*d. Evaluate and categorize as either likely ultimate or proximate cause of dieback*

In the most severe instances of eucalypt dieback closely associated with leaf-feeding insects, the insects should be considered a proximate cause of dieback. The reason for this conclusion is that the prolonged outbreaks result from profound changes to the mechanisms that regulate the insect populations. Therefore, the ultimate cause of these diebacks is the underlying stress agents that trigger and maintain the outbreak (removing either bottom-up or top-down regulators).

*e. Discuss proposed areas of research and potential value of investing in them*

For complex leaf-feeding insect-associated diebacks not involving miners, there is significant research needed to fully examine the hypothesis first outlined by White (1969). First, additional observational studies investigating the association between climate factors, leaf nutrition, and insect outbreaks would help to determine the universality of the hypothesis. Second, experimental and retrospective studies are necessary to examine the causal linkages between climate and edaphic

stressors and insect outbreaks. Third, trials and fully-replicated experimental manipulations aimed at breaking the cycle of defoliation and dieback, and improving eucalypt health are prudent. Since the positive feedback cycle of dieback-resprouting-dieback appears to be relatively consistent in many insect-eucalypt systems, research should focus on either *identifying and preventing the conditions that trigger outbreaks* or *maintaining appropriate top-down regulating mechanisms* in order to quell outbreaks after they start.

For Bell-miner dieback, and other dieback events suspected to involve miner species, trials and research experiments are required to test the hypothesis outlined by Stone (1999) and Stone et al. (2008) regarding the role of lantana and canopy disturbance in creating and maintaining forest structural conditions that are favoured by miners. If the hypothesis is confirmed to be accurate, forest treatment protocols can be developed in order to restore forest patches that currently favour Bell-miners or prevent the creation of more forest in this structural condition. Some combination of active silvicultural- and weed-management will likely be required in order to correct for the current ecological dysfunction. The example of miner-associated eucalypt dieback represents an opportunity to bring largely disparate parties together to take a transdisciplinary approach, including affected communities, conservation and forestry organizations, and experts studying trees, leaf-feeding insects, and birds. To reiterate statements made early, however, these actions are only likely to assist in breaking reinforcing processes, and not prevent Bell-miner dieback

## Nutrient disorders

### *a. Hypothesized mechanisms*

Nutrient disorders, including both deficiencies and excessive nutrients, are a well-known cause of stress in eucalypts (Snowdon 2000). The vast majority of published nutrient disorders concern plantation-grown eucalypts (Dell et al. 2001). This is unsurprising considering that attempts to grow exotic eucalypt plantations are occurring worldwide (Burgess and Wingfield 2017), and eucalypt growth is sensitive to a variety of macro- and micronutrients (Dell et al. 2001). Outside of eucalypt plantations, nutrient dynamics are thought to be involved in the dieback of some rural eucalypts (Landsberg 1990b, Davidson et al. 2007), and those near roadways and urban development (Hanold et al. 2006, Grigg et al. 2009). Here, agricultural practices and urban development alter soil chemistry, which can affect trees directly (Jones et al. 1990), and indirectly by attracting and increasing the development of folivores, including leaf-feeding insects (White 1984, Marsh and Adams 1995). Land-use and land management also intersects with nutrients with respect to agricultural practices and fire. Fire is an important part of terrestrial nutrient cycling in many regions of Australia (Raison 1980, Abbott et al. 1984, Turner and Lambert 2005). The interactions between low-intensity fire, agricultural practices and nutrient dynamics as causal processes in eucalypt dieback are discussed in the following section (*Land-use and management*).

One of the most widespread and severe eucalypt dieback events associated with nutrient disorders is known as Mundulla Yellows (Parsons and Uren 2007), named after a district in South Australia where the disorder was first observed in the 1930s (Parsons and Uren 2011). Symptoms include yellow, chlorotic foliage, and protracted crown dieback (Hanold et al. 2006). The disorder has been observed throughout southeastern Australia (Hanold et al. 2006), commonly on highly disturbed sites, including roadsides (Parsons and Uren 2011) and parklands (Grigg et al. 2009). After multiple failed attempts to isolate potential biotic factors (Hanold et al. 2006, Luck et al. 2006), it seems clear that Mundulla Yellows is a strictly abiotic disorder. Symptomatic eucalypts have been associated with high soil pH and levels of soil carbonates, and reduced levels of available foliar iron (Fe) and manganese (Mn) (Czerniakowski et al. 2006, Grigg et al. 2009). These observations support the theory that Mundulla Yellows caused by lime-induced chlorosis (Parsons and Uren 2007), resulting from limestone dust on roadways or alkaline bore water. The theory is further supported by experimental trials, which have shown that injection with nutrient implants can correct for the deficiency of Fe and Mn, detoxify the alkalinity, and increase canopy greenness and recovery (Schultz and Good 2018). Mundulla Yellows represents another example of how widespread land use and management can alter eucalypt physiology and induce dieback.

As mentioned, and discussed briefly in the *Leaf-feeding Insects* section, foliar nutrients are an important variable in explaining folivore feeding behaviour and success (Ohmart et al. 1985, Casotti and Bradley 1991), and thus many eucalypt dieback events. The sources of high nutrient levels (especially N) in eucalypt foliage are varied and complex. Understanding from where and how nutrient accumulation is triggered in eucalypts may be important for breaking the defoliation-dieback cycle caused by leaf-feeding insects. Principal sources of elevated nitrogen content of eucalypt leaves include drought (Marsh and Adams 1995), agricultural runoff (Granger et al. 1994), and certain fire regimes (Jones and Davidson 2014). Here, we focus on drought (agricultural practices and fire regimes are discussed later). White (1984) highlights the fact that senescing tissues have high levels of soluble amino acids, in an attempt by the plant to move this valuable material to new leaves. Insect herbivores that target dying tissues for herbivory are termed “senescence-feeders” (White 2015b). The relationship between drought stress, high nitrogen concentrations in senescing leaves, and leaf-feeding insect response is likely a common source of the defoliation-dieback positive feedback cycle in some severe dieback events. Moisture stress in eucalypts from drought, or drought combined with heat, is likely an important trigger in intact forest and woodland ecosystems. The gumleaf skeletoniser (*Uraba lugens* Walker) is an example of a senescence-feeding insect with population outbreaks triggered by drought in intact forest ecosystems (Farr et al. 2004).

*b. Primary researchers, institutions and seminal outputs*

A series of researchers from Department of Primary Industries Research in Victoria, including Barbara Czerniakowski, Joanne Luck, Robert Parsons and Rosa Crnov, along with Ian Smith from the

University of Melbourne conducted critical research into the biotic and abiotic causes of Mundulla Yellows dieback. Nick Uren from La Trobe University in Victoria have outlined the theory of lime-induced chlorosis to explain the findings of Czerniakowski and others. Additionally, Dagmar Hanold and John Randals (University of Adelaide) outlined the etiology of the Mundulla Yellows disorder and investigated potential biotic factors. Bernard Dell (Murdoch University) is a world expert of nutritional disorders of eucalypt plantations, and contributed to findings regarding disorders of *E. gomphocephala* along with Giles Hardy (Murdoch University) who has been experimenting with the use of nutrient implants for diagnosing nutrient disorders of eucalypts.

*c. The areas of contention and concerns raised with the causal process*

For years following the first observations of Mundulla Yellows, plant pathologists searched for biotic associates, largely ignoring many of the potential site and abiotic factors associated with the dieback. Later scientists focused on these site and abiotic patterns to determine the factors consistently associated with the disorder. Based on a reading of the literature, there appeared to be some contention between scientists studying potential abiotic and biotic factors in the Mundulla Yellows dieback. It remains unclear whether the contention still exists. However, there remains no clear evidence that biotic factors play a role in this dieback.

*d. Evaluate and categorize as either likely ultimate or proximate cause of dieback*

The Mundulla Yellows dieback provides another example of how landscape-level manipulation of Australian ecosystems can predispose eucalypts to dieback. In this case, land use should be considered the ultimate cause of dieback, while the nutrient disorder should be considered the proximate cause. Lime-induced chlorosis has not been observed in intact native ecosystems.

*e. Discuss proposed areas of research and potential value of investing in them*

Given the mechanism outlined in the Mundulla Yellows line of research, one area of proposed research in native eucalypt ecosystems would be the interaction between climate changes and nutrient disorders in eucalypts. For example, nutrients are transported into plants via roots during water absorption. As precipitation patterns change, and become more erratic, nutrient disorders in eucalypts may become more prevalent during dry periods. Additionally, many eucalypts are dependent on groundwater stored in limestone aquifers. As groundwater stores dry, will nutrient disorders, including those aggravated by increasing alkalinity, including Fe, and Mn deficiencies, become more pronounced? Finally, for the anthropogenically-altered vegetation afflicted by Mundulla Yellows throughout southern Australia, restoration and treatment approaches need to be developed in order to improve the condition of forest and woodland remnants.

## Land-use and management

### *a. Hypothesized mechanism*

Many of the complex and severe eucalypt dieback events are associated with land-use and/or land management practices that deviate from historical patterns (Reid and Landsberg 2000). With widespread European colonization of southern Australia during the 19<sup>th</sup> and early 20<sup>th</sup> century came progressive disfigurement of native ecosystems to accommodate settlement, agriculture, and resource extraction. By the 1970s, many rural regions had been irreversibly altered to accommodate production of agricultural and timber commodities and scientists began to suspect land alteration as a driving factor in eucalypt dieback. Simultaneously, observation and documentation of eucalypt dieback likely increased as remaining trees in paddocks and surrounding patches of forest undoubtedly received increased scrutiny from farmers and resource managers. The primary land use and land management changes most frequently associated with eucalypt dieback events include fragmentation (Jones et al. 1990), altered fire regimes, grazing and other more intensive agricultural practices (Davidson et al. 2007).

Fragmentation of native vegetation results in a wide array of associated changes to physical (Saunders et al. 1991) and biological factors (Hobbs 2001), which clearly impact tree functioning and condition. Extensive surveys of the New England Tablelands region found that the severity of eucalypt dieback was consistently associated with severe fragmentation (Jones et al. 1990). Reid and Landsberg (2000) highlight that areas that have undergone the highest levels of modification have experienced the greatest severity of dieback. These observations are supported by extensive retrospective surveys outside of NSW in Tasmania (Davidson et al. 2007), and landscape analyses in Western Australia (Brouwers et al. 2013). Fragmentation dramatically alters radiation fluxes and the water cycle (Saunders et al. 1991). These alterations can affect trees directly by exposing them to potentially damaging extremes, including both high and low air temperatures and soil moisture availability. Trees that have grown and matured under a stable water regime and moderated air temperatures as part of an intact canopy are suddenly exposed to radical moisture and temperature regime shifts following clearing (Murcia 1995). Historic drought and heatwaves act to compound the stressful conditions (Landsberg 1985). These microsite changes in climate can also impact eucalypts indirectly, since pests, including leaf-feeding insects also respond to the altered environment and tree condition, commonly to the detriment of the host (Landsberg and Wylie 1983). Additionally, fragmentation alters the distribution of beneficial mycorrhizal associations, which can indirectly affect tree health (Sapsford et al. 2020). Fragmentation is a clear associated factor of the most severe dieback events in rural Australia. A long-term forest fragmentation field experiment in southeastern NSW has demonstrated that eucalypts along fragmented edges experience altered microclimate and high rates of stress and increased mortality (compared to intact forest), especially within the first 4 years post-clearing (King et al. 2018). While the experiment is not examining the extreme

fragmentation observed in many areas of rural Australia (Margules 1992), it illustrates the pronounced role of edge effects and effects environmental changes have on eucalypt growth and mortality. Given the number of environmental changes associated with fragmentation, that can have a variety of direct and indirect effects on eucalypt health, it greatly complicates diagnosis of dieback events.

Agricultural practices in rural southern Australia, especially the production of livestock, is also consistently associated with severe eucalypt dieback events in rural areas (Mackay et al. 1984, Heatwole and Lowman 1986, Davidson et al. 2007). Livestock grazing and associated practices, independent of fragmentation, can have a variety of indirect effects on eucalypt health. First, grazing animals compact soil and defecate beneath tree canopies dramatically altering soil properties (Yates et al. 2000). These changes include increasing the bulk density, decreasing porosity and water-holding capacity and increasing nutrient content, especially nitrogen (Braunack and Walker 1985, Davidson et al. 2007). Agricultural practices also commonly include fertilization of pastures. Both grazing and fertilization can directly impact eucalypt health by flooding eucalypts with excessive nitrogen, inducing severe dieback. Several studies have attributed failing eucalypt canopies to excess nitrogen in the absence of biotic pests in rural regions of southeastern Australia (Granger et al. 1994, Davidson et al. 2007). More commonly, leaf-feeding insects respond to excess nitrogen in trees, however, resulting in outbreaks (Reid and Landsberg 2000). In this way, agricultural practices represent another trigger for insect outbreaks, and the dieback-resprouting-dieback positive feedback cycle. Excess nutrients arising from agricultural practices can also have profound shifts on the mycorrhizal community. Mycorrhizas provide critical services to eucalypts, including assisting with water and nutrient absorption, and protection from root disease. Excessive soil N results in shedding of mycorrhizal associations. Therefore, eucalypts exposed to high soil N can be more susceptible to drought and root pathogens. Perhaps the largest environmental change from agricultural practices is displacement of perennial understory vegetation with annual vegetation. This replacement has implications for evapotranspiration and soil erosion, which both increase under grazing (Yates et al. 2000). Collectively, these alterations to the landscape from agricultural practices surrounds established eucalypts in an alien environment, and subjects them to a wide variety of novel direct and indirect stressors.

Altered fire regimes (i.e. changes to fire frequency, intensity, season), has also been proposed as a cause of dieback in eucalypts (Jurskis and Turner 2002, Jurskis 2005a, Turner and Lambert 2005, Close et al. 2009). These studies highlight the changes in fire regimes (i.e. frequency and intensity) that have occurred in many eucalypt-dominated ecosystems since European arrival (Gammage 2012, Pascoe 2018). Across southern Australia, charcoal records indicate substantial fire activity in the last 40,000 years, an increase at initial European arrival, followed by a decrease (Bradstock et al. 2002, Gammage 2012). Due to urbanization, fragmentation, and changing land management practices, fire frequency has decreased across a variety of ecosystems (Bradstock et al. 2002). Such patterns have

been documented across a range of ecosystems worldwide where Indigenous populations who commonly applied fire were displaced by Europeans who did not include fire in their land management practices, and in many cases purposively excluded fire (Carle 2002); (Pascoe 2018). These changes are known to cause shifts in ecosystem functioning, composition, and structure (Bradstock et al. 2002). Researchers have hypothesized that fire regime shifts lead to altered nutrient and water cycling, undermining eucalypt health and causing persistent eucalypt dieback events (Close et al. 2009, Close et al. 2011, Jones and Davidson 2014).

Two ecosystems that have experienced widespread and severe eucalypt dieback events have been used to develop hypotheses related to fire regime change and dieback. Specifically, dieback in *E. delegatensis* and *E. coccifera* in the highlands of Tasmania (Ellis 1971, Harvest et al. 2008, Close et al. 2011) and in *E. gomphocephala* in southwestern Australia (Archibald et al. 2010, Close et al. 2011) have both experienced dieback and long-term shift in fire regime. In both ecosystems, the effects of altered fire include the development of a dense woody understory (Harvest et al. 2008, Close et al. 2009, Jones and Davidson 2014); however, all three species are associated with wetter conditions where longer fire intervals and fires with a greater proportion of high severity fire would be anticipated. None of these tree species are associated with grassy understories indicative of frequent, low-severity fire regimes. In *E. gomphocephala* forest, there is some indication that trees experiencing fire regime shifts have also been under more water stress (Close et al. 2009), and long-unburnt *E. delegatensis* forests have significantly altered macro-nutrient pools (N and P) (Jones and Davidson 2014). Close (2009) hypothesized that understory competition, arising from lengthening of fire interval, decreases the availability of soil water for overstory trees, leading to dieback. However, a study of *E. gomphocephala* found that over two years of monitoring, it did not experience severe and irreversible water stress, and trees opportunistically used groundwater when surficial soil water was limiting (Drake 2008). These findings, along with the fact that (Close et al. 2011) examined a small number of sites, and other findings from an extensive vegetation survey that found that trees on “healthy” and “dieback” sites had similar understories (Wentzel et al. 2018), erode support for the hypothesis. In *E. delegatensis*, the relationships between fire regime shifts and eucalypt health is clearer as (Ellis et al. 1980) observed an improvement in *E. delegatensis* 10 years following treatment with felling midstory and low-moderate severity burning of the understory.

Nitrogen accumulation in eucalypt ecosystems, and its role in disrupting ecological functioning and tree health, has been discussed extensively in the literature (Jurskis and Turner 2002) (Turner et al. 2008, Christie and York 2009, Horton et al. 2013, Turner and Lambert 2016). There is evidence that N accumulates in the soil of Australian forests in the absence of fire for extended periods (>10 years), through the process of N-fixation (Turner et al. 2008), and that soil N occurs at low-levels in frequently-burned forest (Muqaddas et al. 2015). Jurskis and Turner (2002) hypothesize that soil N, accumulating under eucalypts experiencing fire exclusion, is translocated to foliage and

triggers outbreaks of leaf-feeding insects. In addition, they hypothesize that the compositional and structural effects of fire exclusion, including a dense, tall understory and midstory, provide habitat for Bell-miners. They imply that these changes would not occur if forest was burned more frequently. Indeed, studies of eucalypt dieback and fire patterns have observed elevated N in soil and foliage of affected trees (Jones and Davidson 2014); however, others have found no relationships between affected trees with elevated N (Christie and York 2009, Close et al. 2011). Christie and York (2009) examined the hypothesis in a replicated field experiment. In that experiment, (Christie and York 2009) found no support for the hypothesis, including that fire frequency failed to explain differences in foliar content of C and N, and no significant differences in herbivory were observed across fire treatments. These findings, however, may not be capable of fully dismissing the hypothesis proposed by Jurskis and Turner (2002) for multiple reasons. These include the fact that the experimental study suffered from a small number of plots (Christie and York 2009), foliage-feeding by insects in the studied eucalypt species, *E. pilularis*, is much less common compared to others (Stone et al. 1998), and foliar nutrients and insect feeding, both known to be dynamic processes, were measured at one point-in-time. At this point, the link between fire frequency, nutrient dynamics, and eucalypt dieback events remains unresolved.

*b. Primary researchers, institutions and seminal outputs*

Many scientists across Australia have active research programs in fire, fire management and fire ecology and are too numerous to enumerate here. Rather, we would highlight those scientists whose work has focused on the ecological impacts of planned fire, its frequency, and the dimensions of environmental decision making relative to forest management. Examples include drought-fire feedbacks (Luke Collins, Latrobe University, Rachel Nolan and Matthias Boer Western Sydney University), nutrient pools relative to fire interval (Lauren Bennett, University of Melbourne; Tina Bell, University of Sydney), fire regime simulation relative to vegetation and bushfire hazard with explicit focus on spatial pattern and optimised management strategies (Trent Penman, University of Melbourne; Owen Price and Ross Bradstock, University of Wollongong; Geoff Cary, Australian National University).

*c. The areas of contention and concerns raised with the causal process*

The primary debate resides in the role of altered fire frequency in explaining eucalypt dieback. More specifically, whether the hypothesis proposed by Jurskis and Turner (2002) is true, and if so, the universality of it in explaining eucalypt diebacks continent-wide (as proposed by Jurskis 2005). As discussed above, multiple aspects of the proposed effects of altered fire regimes have merit, including that fire regimes in many ecosystems have changed since European arrival, and lengthening of the fire-free period (mesophication) can lead to substantial compositional and structural changes in many ecosystems (Nowacki and Abrams 2008), particularly those adapted to

frequent fire (Covington and Moore 1994, Gilliam and Platt 1999). The primary facet of the hypothesis that is lacking is a strong causal tie to multiple eucalypt dieback events. On this, the research has been mostly lacking. Of those studies that do exist, including (Ellis et al. 1980), Close et al. (2011), and Christie and York (2009), the findings are mixed.

*d. Evaluate and categorize as either likely ultimate or proximate cause of dieback*

The land-use and land management changes that have been most closely associated with eucalypt dieback, fragmentation, agricultural practices, and altered fire regimes, would be considered ultimate causes of dieback, since they can either cause dieback directly, or indirectly lead to dieback through a series of other stressors and processes.

*e. Discuss proposed areas of research and potential value of investing in them*

In our view, the effects of fragmentation on eucalypt ecosystems has been relatively well-studied. In the absence of widespread restoration of many severely fragmented regions, the residual trees are likely to continue to experience severe dieback events, as fragmentation increases with continued tree mortality. Since land management practices have the ability to be altered, in an effort to improve eucalypt health, research investment in this area could make substantive impacts on stemming current and future eucalypt dieback events. We recommend examining the hypotheses related to the role of altered fire regimes in eucalypt dieback events. In light of the recent 2019-2020 bushfire season and, over the last decade, a growing advocacy of Indigenous burning practices monitoring of eucalypt canopy condition in areas treated with traditional burning would be useful. More specifically, we recommend investigating the causal relationships, through hypothesis testing, between the frequency of surface fire, nutrient cycling, and leaf-feeding insect herbivory in eucalypt forests and woodlands.

## Other stressors

A variety of stressors of eucalypts were not addressed in full, due to the low frequency with which they have been implicated in widespread, and severe eucalypt dieback events in southeastern Australia, especially NSW. These include, fungal foliar pathogens, shoot and stems pathogens, woodboring insects, root pathogens, mycorrhizal fungi, and frost. Many of these stressors react to changing tree health and climate conditions, and have the potential to become more important in the future.

Fungal foliar pathogens of eucalypts cause necrotic leaf spots, which results in reduced photosynthesis, and commonly premature abscission (Abbott et al. 1993). The primary leaf diseases affecting eucalypts in Australia include *Mycosphaerella* leaf disease (family *Mycosphaerellaceae*) and *Teratosphaeria* leaf blight (family *Teratosphaeriaceae*) (Burgess and Wingfield 2002, Carnegie 2007,

Andjic et al. 2019). While the ultimate effect of defoliation by foliar fungi is reduced growth (Carnegie and Ades 2003), repeated defoliation has the potential to trigger a cascade of events, including parasitism by opportunistic insect and canker fungi that can ultimately result in tree mortality (Carnegie 2007). This process is, however, restricted to plantations and has not been observed in native forests (Burgess and Wingfield 2002). Foliar fungi have largely not been considered important contributors to eucalypt dieback of mature trees. However, with continued climate change, these pests have the ability to increase their incidence and severity since their populations are largely contingent on the growing environment and host defense.

A wide variety of pathogens cause cankers in shoot and stem tissues, leading to eucalypt dieback (Davison and Tay 1983, Old et al. 1986, Burgess et al. 2005, Carnegie 2007). Most species are fungal endophytes, or latent pathogens, that cause cankers only when triggered by other stressors (Old et al. 1990, Carnegie 2007, Nadolny 2008). Shoot and stem pathogens have been associated with complex diebacks, including that of *E. wandoo* (Hooper and Sivasithamparam 2005), *E. gomphocephala* (Chilcott 1992), and rural dieback of *E. blakelyi* (Old et al. 1990). In most cases these pathogens cause low levels of dieback in isolated regions (Carnegie 2007), or cause severe cankers but have low incidence (Yuan and Mohammed 1997, Pascoe et al. 2018). One notable exception is *Quambalaria coyrecup*, which causes canker of native *Corymbia* in southwestern Australia (i.e. “Marri canker”), which is widespread throughout southwestern Australia (Paap et al. 2017b) and leads to severe eucalypt dieback and tree mortality over multiple years (Paap et al. 2017a). Additionally, an invasive rust pathogen and causal agent of myrtle rust (*Puccinia psidii*) was introduced to the mainland of NSW in 2010 (Carnegie et al. 2010). *Puccinia psidii* is a known primary pathogen of eucalypts outside of Australia, and causes crown dieback and tree mortality in a variety of the Myrtaceae (Arriel et al. 2013). Since its introduction to Australia, however, there are limited published reports of its effects on eucalypts (Carnegie 2015). Given the lack of published accounts of myrtle rust effects, combined with uncertainty surrounding eucalypt susceptibility of the introduced strain (Lee et al. 2015), the role myrtle rust will play in eucalypt dieback events in the future is unclear. In summary, a variety of opportunistic fungal pathogens cause tissue damage to shoots and stems, when triggered by other stressors, leading to eucalypt dieback. Like foliar fungi, the behaviour of these pathogens is likely to change with continued climate changes. Since many are latent pathogens, changes in host condition with climate change are very likely to influence the expression of disease symptoms.

Woodboring insects, including woodboring Coleoptera (mainly Cerambycidae and Buprestidae) and Lepidoptera (mainly Cossidae and Hepialidae) can cause stem damage to living eucalypts (Lawson and Debuse 2016), and outbreaks occasionally have been associated with eucalypt dieback events in the southern Tablelands (Pook and Forrester 1984) and southwestern Australia (Hooper and Sivasithamparam 2005, Seaton et al. 2015). Most woodboring insects either feed on dead trees or the heartwood and roots of eucalypts (Lawson and Debuse 2016), and are not associated

with eucalypt dieback. They are considered economically-relevant pests, however, as they can degrade timber quality (Creffield et al. 1995, Peters et al. 2002). The subset of woodboring beetles that have been associated with eucalypt dieback in Australia feed in the phloem and xylem of stems and branches compromised by other stressors (Hooper and Sivasithamparam 2005, Wotherspoon et al. 2014, Seaton et al. 2015). White (2015a) has found that when stressed by drought, concentrations of nutrients in phloem allow for rapid development of phloem-feeding beetles, and has classified them as senescence feeders (White 2015b). These findings are supported by observations made in native forests of southwestern Australia and eucalypt plantations in southeastern Australia where woodboring beetles preferentially attack drought-stressed trees (Abbott et al. 1991, Farr et al. 2000, Wotherspoon et al. 2014, Seaton et al. 2015). When woodboring insects are associated with eucalypt dieback, they should be considered a proximate cause of dieback. Since woodboring insects respond to changing drought and fire disturbance patterns (Elliott et al. 2019), we can expect population increases with the continuation of current drought and fire trends in Australia, though this has not yet been quantified. What remains unclear is how increased populations will affect the frequency and severity of eucalypt dieback events, if at all.

While many suspected root pathogens have been isolated from eucalypts exhibiting dieback symptoms throughout southern Australia (Cunningham et al. 2010, Burgess et al. 2017b, Khaliq et al. 2019), including many in the urban environment or other severely modified ecosystems (Rea et al. 2010, Barber et al. 2013, Aldaoud et al. 2016), few have shown the ability to cause widespread dieback in mature trees in more natural ecosystems (Kile 1981, Shearer et al. 2007). *Phytophthora cinnamomi* and *Armillaria luteobubalina* are the two primary exceptions. Both species are associated with deaths of eucalypts in southwestern Australia (Podger 1972, Tippett et al. 1983, Shearer and Tippett 1988, Shearer et al. 1997) and portions of Victoria (Podger et al. 1978, Kile 1981, Weste et al. 2002, Weste 2003). Recent modelling and field sampling show a high likelihood of presence of *P. cinnamomi* throughout much of coastal southern Australia, including NSW (Burgess et al. 2017a). However, rarely has it been associated with eucalypt dieback in this region (McDougall 2005). In NSW, its' effects on eucalypts appear to be predominately restricted to plantation settings, where young trees on sites prone to waterlogging can be infected (Carnegie 2007). *Armillaria luteobubalina* is widely dispersed in southeastern Australia, but mainly acts as a saprophyte of dead and dying hosts, including many eucalypts (Kile and Watling 1981). Root pathogens have the potential to cause dieback in eucalypts. However, they are currently not primary factors in widespread and severe dieback events in NSW. This, as with other pathogens, has the potential to change, however, especially with increased urbanisation, plant movement, and climate change.

Most eucalypts in native ecosystems associate with soil borne fungi to form mycorrhizal associations that are beneficial to the host tree (Malajczuk et al. 1982). Mycorrhizas assist in extracting and transporting nutrients from nutrient-limited Australian soils (Marschner and Dell 1994). In several examples, a change in the composition of mycorrhizal communities has been

associated with eucalypt dieback (Anderson et al. 2010, Horton et al. 2013, Ishaq et al. 2013, Sapsford et al. 2017, Ishaq et al. 2018, Sapsford et al. 2020) or drought-induced dieback (Hopkins et al. 2018). Eucalypt trees exhibiting dieback symptoms can have fewer fine roots and mycorrhizal associations compared to nearby non-symptomatic trees (Scott et al. 2012). Specifically, colonization of seedling roots by ectomycorrhizal (ECM) fungi was higher in soil taken from healthy *E. gomphocephala* canopies in southwestern Australia, and arbuscular (AM) fungi dominated roots in soil from sites with declining canopies (Ishaq et al. 2013). It remains unclear, however, whether changes to mycorrhizal associations represent a cause or effect of eucalypt dieback (Sapsford et al. 2017, Ishaq et al. 2018). For example, observed changes in mycorrhizal communities (Anderson et al. 2010) and abundance (Scott et al. 2012) are thought to be an effect of *Phytophthora* infestation and subsequent fine root loss of eucalypt hosts in southwestern Australia. In southeastern Australia, (Horton et al. 2013) postulates that changes to soil chemistry are driving both mycorrhizal community changes directly and indirectly by increasing eucalypt dieback, and therefore classifies mycorrhizal changes as an effect. Indeed, experimental studies have shown that changing soil nutrients, especially nitrogen, can cause changes to mycorrhizal associations (Mason et al. 2000). Another hypothesis that has been proposed involves declining eucalypts being associated with a loss of digging mammals and the mycorrhizal fungi they vector across the landscape. The loss of these mammals across Australia, due to habitat clearing and the introduction of predators such as cats and foxes, has resulted in many fungi, including hypogeous (underground) mycorrhizal species not being transported in scat (Tay et al. 2018) across the landscape, with possible implications for plant establishment (Valentine et al. 2017) and growth (Dundas et al. 2018, Valentine et al. 2018). At this point, there is no direct evidence that mycorrhizal changes *per se* are causing eucalypt dieback. Additional experimental studies are warranted to elucidate the nature of the relationship between mycorrhizas, vectors, eucalypt dieback, and other causal factors.

Frost has the ability to cause widespread dieback in eucalypts, with damage ranging from miner leaf scorch to complete tree dieback (Davidson and Reid 1987). Rarely does frost kill mature eucalypts outright, rather repeated events can cause crown dieback and degradation (Matusick et al. 2016b). Significant dieback from frosts have been recorded from high elevation forests in Tasmania (Davidson and Reid 1985) and Victoria (Bond 1945, Banks and Paton 1993), the mallee region of Victoria (O'Brien 1989), plantation forests in ACT (Thomson et al. 2001), and forests (Quain 1964, Matusick et al. 2014) and open eucalypt woodlands (Matusick et al. 2016a) in southwestern Australia. Recovery from frost damage can take 5 years or more (Banks and Paton 1993). Therefore, the frequency of severe frosts is an important factor in whether trees recover, or experience repeated dieback and crown decline (Matusick et al. 2016b). Since there is a high variability in tolerance to frost among eucalypts (Larmour et al. 2000), it can be an important driver of tree distributions in certain locations (Davidson and Reid 1985). Frost damage in Australia is mainly confined to mountainous areas, and Mediterranean-type climate zones. In these areas, radiative frosts are

common, which form from pooling of locally cold air on clear winter nights (Aston and Paton 1973, Banks and Paton 1993). Since heavy cold-air pools on clear winter nights, radiative frost damage is strongly associated with topographic position, including valley bottom, dune swales, and lower slope positions (Davidson and Reid 1985, Banks and Paton 1993, Matusick et al. 2014). Under an atmosphere enriched with CO<sub>2</sub>, some eucalypts are likely to be more susceptible to frost damage, and it is currently unclear whether atmospheric CO<sub>2</sub> or average temperatures will have more effect on future frost damage (Woldendorp et al. 2008). Global- and regional-scale climate models predict less frequent and severe frost events under future warming scenarios. However, radiative frosts in Australia are driven by local atmospheric decoupling, and are governed by local topographic factors instead of region-scale air-masses (i.e. convective frosts common in North America) (Daly et al. 2009). Therefore, findings from global- and regional-scale models cannot reliably predict radiation frosts in Australia (Daly et al. 2009). Indeed, regions of southeastern and southwestern Australia have experienced changes in frost patterns, including increases in frost frequency corresponding with atmospheric warming in recent decades (Crimp et al. 2015, Zheng et al. 2015, Matusick et al. 2016b). For example, Crimp (2016) found that frost season length has increased by 26 days (in 2014), on average, in southern Australia, and some areas experience their last frost four weeks later than in the 1960s. While frost is not currently an important cause of widespread and severe dieback events, this could change under continued climate change.

## Summary

From our intensive review of the literature, it seems clear that eucalypt dieback events can be induced by a wide variety of causal stressors. It also seems clear that the stressors capable of causing widespread and severe eucalypt dieback events, especially in NSW, are finite and are limited to predominantly abiotic sources of stress, including stress induced by fire, drought, waterlogging, nutrient disorders, and land-use and management change. Leaf-feeding insects are very responsive to specific weather patterns directly, or indirectly from the absence of bottom-up or top-down regulating factors. The foliage feeding insects are therefore nearly always considered proximate causes of dieback, and represent an important and sensitive indicator of ecosystem dysfunction. Intact, functioning ecosystems have the negative feedbacks capable of controlling leaf-feeding insect outbreaks, and maintaining tree and forest condition. Most of the important causes of eucalypt dieback in NSW are related to anthropogenic changes. This is unsurprising considering the substantial level of landscape modification in NSW and surrounding states over a relatively brief timespan since European settlement. The number of ecosystem processes altered, and their inherent relatedness, makes accurately diagnosing eucalypt dieback a daunting challenge, and one that is very likely to continue as urbanization and climate change continue to alter Australian ecosystems.

We believe that much of the historical contention surrounding eucalypt dieback can be explained by a philosophical divide among researchers, foresters, and the broader concerned community. There appears to be groups of individuals that believe that eucalypt dieback is a single phenomenon, which can be explained by a single model. This perspective may be understandable given the apparent increase in incidence of eucalypt dieback nationwide since the 1970s, and the many common associated changes that have occurred nationwide, including urbanization, climate change, and changing land management practices. Other groups of individuals appear to clearly emphasize the uniqueness of each dieback, focusing on the individual causal factors with the highest probability of being associated, and forming tailored hypotheses for the circumstance. From our review, it seems clear that there is no “global model” that can describe eucalypt dieback. The situations in which eucalypt dieback events have been observed vary considerably in their circumstances, and there are few clear unifying factors. It is important to realize that crown dieback is a generic reaction to stress by eucalypts, and most other angiosperms. Most stressors of sufficient strength, singly or in combination, elicit crown dieback in broadleaved trees, and therefore the conditions which result in dieback events can vary considerably from one to another. Despite this perspective, there are several generalizations that appear evident from this collection of studies and are outlined below.

- 1) Widespread and severe dieback events may occur in any system spanning gradients of anthropogenic change, species, climate, and edaphic setting.
- 2) While events may occur in any system, fragmented and highly altered systems do appear to have greater vulnerability and prevalence of dieback events. Loss of stabilizing processes and introduction of novel stressors (elevated nutrients, waterlogging, weeds, introduced pathogens, logging legacy effects) are implicated in elevated vulnerability.
- 3) Processes and impacts interact. Because of the multi-factor, complex nature of these diebacks, we strongly advocate multi-disciplinary and integrated approaches to the study of these phenomena. A narrow disciplinary view (fire, physiology, entomology, pathology, etc) in isolation risks missing important clues and identifying ultimate causation and thus appropriate management action.
- 4) Climate change itself exercises direct and indirect effects and events will become more frequent. Direct effects of changing climate (drought, heat waves, warm winters) will become more frequent and so will indirect effects (bushfire, unseasonal fire, pest life cycles, etc). This means greatly elevated risk and vulnerability to frequent disturbance and reduced time for ‘recovery’. Therefore, science, and Indigenous knowledge should explore the implications of disturbance interactions and implications for management and maintenance of ecosystem services.

Our review has highlighted a variety of potential research investments for each of the causal factors most important to NSW. The list of potential research is not intended to be comprehensive.

Rather, we have attempted to narrow the list to those research topics that are most likely to yield either substantive advancements in our understanding of eucalypt dieback or, ideally management solutions. The potential research investments we have discussed in each section are briefly outlined below.

#### *Fire*

- Fire effects studies that fuse data from field-based plots with remote sensing, spanning from stand- to landscape-scales, aimed at developing empirical relationships necessary to improve predictions.
- Systematic observational and experimental studies that seek to determine the relative resistance and resilience among co-occurring species, which is necessary to predict fire effects under future climates. Quantification of how tolerance varies among species.
- Studies that explicitly seek to understand the effects of compounding disturbances (multiple disturbances occurring in conjunction or in sequence). In particular, with the rich remotely sensed datasets now available, opportunities exist to investigate recorded incidences of dieback, fire, and other drivers (land management, drought, heat waves, insect outbreaks, etc).

#### *Drought and heat waves*

- Studies that seek a fundamental and mechanistic understanding of which species and attributes are capable of resisting and recovering from water stress
- Differentiation of chronic and acute water stress impacts on dieback prevalence and extent
- Systematic efforts to detect and document eucalypt dieback, especially drought-induced dieback
- Retrospective analyses to determine the role of drought in triggering eucalypt dieback
- Research aimed at deciphering the interactions between drought and other stressors, especially leaf-feeding insects.

#### *Waterlogging*

- Expanding and updating modeling research aimed at determining the water availability necessary to maintain the health of floodplain forests.
- Determining the relative susceptibility of species and traits to waterlogging and salinity necessary to assess risk and guide restoration and management.
- Developing the empirical relationships necessary to predict waterlogging and salinity stress under future climate change scenarios.

#### *Leaf-feeding Insects*

- Observational studies targeting associations between climate factors, leaf nutrition, and insect outbreaks.
- Experimental and retrospective studies to examine hypotheses that have been developed to explain causal linkages between climate, edaphic stressors and outbreaks.
- Trials and fully replicated experiments designed to test options for breaking the cycle of defoliation and dieback.
- Through experimentation, testing the hypothesis developed by Stone (1999) regarding the role of lantana in ecosystem dysfunction in northeastern NSW.

#### *Nutrient Disorders*

- Modelling studies seeking to understand how continued climate drying will interact with nutrients to cause dieback, especially those aggravated by increasing alkalinity.

#### *Land-use and management*

- Examine prevalent hypotheses regarding the role of altered fire regimes, including Aboriginal cultural burning regimes, in changing biogeochemical processes, soil biota and their combined ability to cause eucalypt dieback.
- If possible, retrospective studies gathering further evidence of past fire regimes to inform future management. These could include evidence-based investigation of cultural history (oral histories of pre-European Aboriginal land management) as well as dendro-chronological work attempting to find new ways to generate evidence of past fire and climate.

Finally, future and ongoing research should strive to achieve strong inference regarding ultimate drivers of eucalypt dieback. Work identifying ultimate drivers will be the best placed to inform land managers and aid in foreseeing future events. Research with strong inference will have an interdisciplinary team with a sound experimental design that goes beyond observational and correlative approaches and embraces multiple lines of evidence.

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